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Genetic Map of *Saccharomyces cerevisiae*, Edition 9

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INTRODUCTION

The yeast *Saccharomyces cerevisiae* is currently widely used for biochemical, molecular, and genetic research. Besides its traditional importance in the baking and brewing industries, it is increasingly being utilized for the industrial production of recombinant deoxyribonucleic acid (DNA) products. The ease by which this yeast can be genetically and molecularly manipulated, coupled with its extensive genetic map, have made it particularly suitable for use in both research and industry.

In this review we present a new edition of the genetic map of *S. cerevisiae*, edition 9. Included are all pertinent data on genes mapped since our publication of the map in 1980 (132) and data on revisions of previously mapped genes. This review, as was our previous one, is based on both published mapping data and unpublished data kindly supplied by many researchers. We have decided to call the current genetic map edition 9, since there have been eight previous editions partially or wholly emanating from this laboratory. Editions 1 to 8 appeared between 1960 and 1984 (69, 70, 129–132, 135, 136). In addition to these editions, several genetic maps were published by the Lindegren group (77, 78, 105–107, 165), including the first genetic map of *S. cerevisiae* (106). Numerous other versions of the genetic map with minor changes have been published by us and others.

The new molecular biological techniques being used for studies on *S. cerevisiae* yield information about the genome not previously available; because of this, questions arise as to what should be placed on the genetic map and what types of information should be used. The vast majority of genes on the current map have been identified by the phenotype(s) of mutations and have been placed on the map by tetrad analysis. In addition, some genes have been placed on the map by using only aneuploid or mitotic recombination analyses (see Discussion). Some regions, such as the ribosomal ribonucleic acid (RNA) coding region (rDNA) (150) and some of the Ty1 transposon sequences (92), have been included on the map even though they have not been mutated; however, these sequences were mapped by tetrad analysis, using either restriction site polymorphisms or integrated plasmids containing scorable markers. Regions containing open reading frames, even if they have been shown to be transcribed, have not been included on the map unless these regions have been shown, by disruption or deletion analysis, to have a phenotype. Some Ty1 sequences which have been genetically mapped (92) have been included, whereas others which have been identified only by recombinant DNA techniques have not. Since Ty1 sequences transpose and are found in different numbers and positions in different strains (18, 48), the map position of a Ty1 element should be considered tentative. Although to a lesser extent, restriction site (142, 150) and chromosome size (G. F. Carle and M. V. Olson, Proc. Natl. Acad. Sci. U.S.A., in press) polymorphisms have also been found between different laboratory strains of yeasts. Therefore, the distances between genes and possibly even the relative position of genes may vary between different strains. Determination of the order of closely linked clusters of genes by tetrad analysis is usually very difficult. Recently, the order of some clusters of

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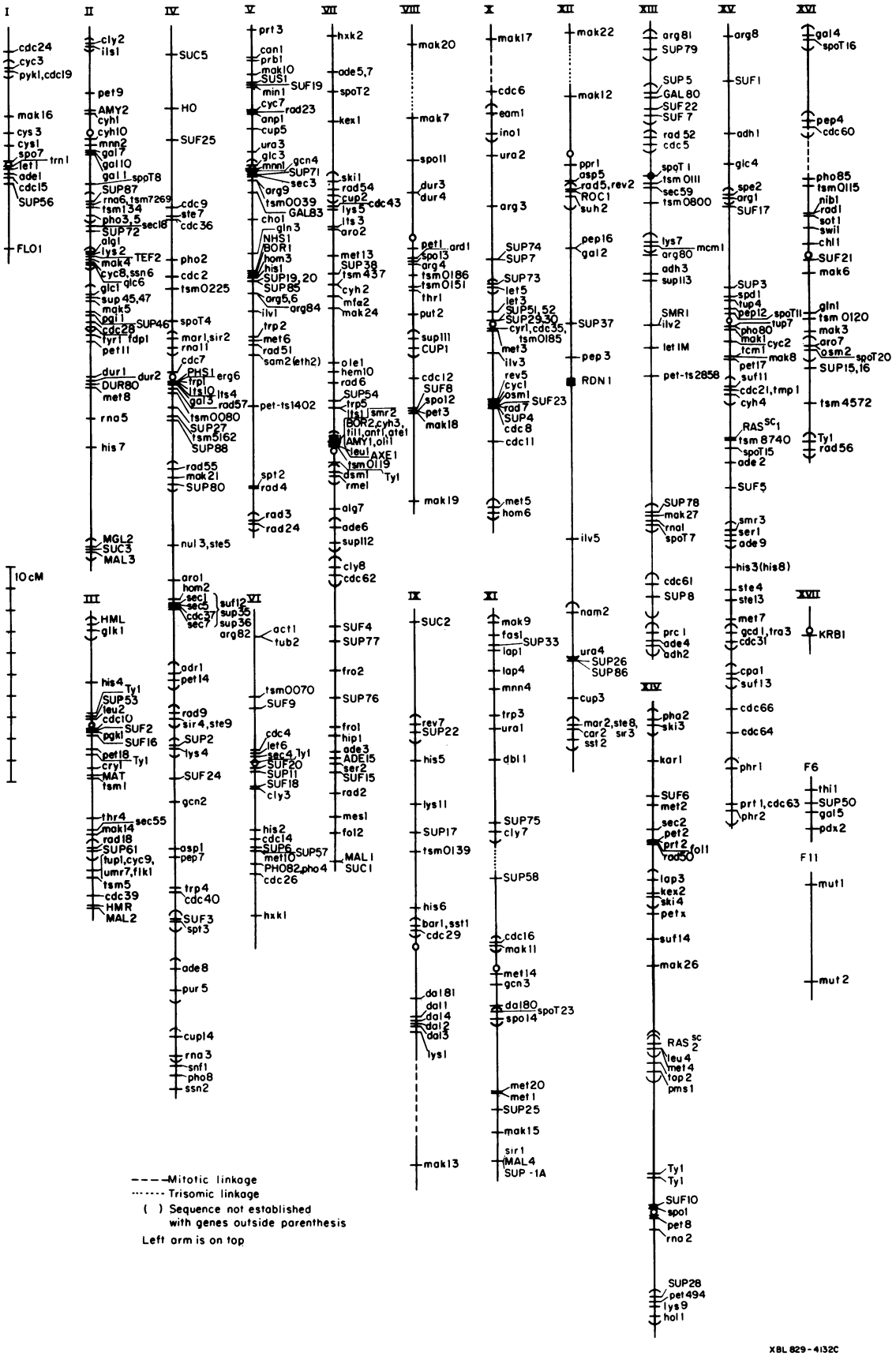
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
XIII
XIV
XV
XVI
XVII
10cM
Mitotic linkage
Trisomic linkage
( ) Sequence not established with genes outside parenthesis
Left arm is on top
XBL 829-4132C

TABLE 1. New tetrad analysis data for chromosome I[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
cdc24-mak16			26	0	40	30.7	3.3	85
cdc24-pyk1			237	0	64	10.7	1.2	85
cdc24-cys1			56	12	162	54.6	6.4	85
cdc24-ade1			66	17	232	56.9	5.5	85
pyk1-mak16			41	0	19	16.3	3.4	85
pyk1-cys1			67	11	144	51.0	6.5	85
pyk1-ade1			78	18	207	57.2	6.5	85
mak16-cys1			15	1	11	34.9	18.5	85
mak16-cen1	43	43				30.3	4.4	85
mak16-ade1			39	4	52	43.2	9.4	85
cys1-spo7			52	0	2	2.4	2.5	R. E. Esposito and C. W. Waddell, personal communication
cys1-cen1	23	5				9.4	4.0	85
cys1-ade1			201	0	62	11.9	1.4	85
cys1-ade1			42	1	8	16.6	13.0	R. E. Esposito and C. W. Waddell, personal communication
cys1-ade1			41	0	3	3.5	2.1	147
Total			284	1	73	11.0	1.4	
cys1-cys3			15	0	2	6.0	4.3	147
cys3-ade1			22	0	8	14.3	5.1	147
spo7-cen1	69	1				0.7	0.6	R. E. Esposito and C. W. Waddell, personal communication
spo7-ade1			64	0	13	8.8	2.5	R. E. Esposito and C. W. Waddell, personal communication
trn1-cen1	548	6				0.5	0.2	C. Cummins and M. Culbertson, personal communication
trn1-ade1			501	0	45	4.2	0.6	C. Cummins and M. Culbertson, personal communication
cen1-ade1	77	8				4.8	1.7	85
cen1-ade1	58	4				3.3	1.6	101
cen1-ade1	500	45				4.2	0.6	C. Cummins and M. Culbertson, personal communication
Total	635	57				4.2	0.5	
SUP56-cen1	51	11				9.3	2.7	101
SUP56-ade1			58	0	7	5.4	2.0	101
FLO1-ade1			58	6	106	43.6	5.7	169

[a] FD, First-division segregation; SD, second-division segregation. These segregations are determined by examination of the segregation of a marker relative to that of a known centromere-linked marker (131, 134).

FIG. 1. Genetic map of *S. cerevisiae*, based on the data presented in Tables 1 through 17, in our earlier reivew (132), and in the text. Centromeres are represented as circles, and the left arm of each chromosome has arbitrarily been drawn above the centromere. Solid lines are drawn to scale and represent linkage distances established by tetrad analysis. The dashed and dotted lines represent linkages established by mitotic and aneuploid analysis, respectively. They have arbitrarily been assigned a minimum distance of 100 cM (see text); these intervals are not drawn to scale. When the orientation of two or more genes relative to outside markers has not been determined, these genes are enclosed within parentheses.

TABLE 2. New tetrad analysis data for chromosome II[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
cly2-AMY2			43	1	59	31.7	3.8	199
cly2-cen2	111	133				34.0	2.8	130, 199
cly2-gal1			25	13	65	115.5	58.7	130
AMY2-cen2	60	21				14.0	2.9	199
AMY2-gal7			62	0	30	16.6	2.6	199
spoT8-pho5			31	0	13	15.4	4.0	191
spoT8-lys2			49	1	38	25.3	4.5	191
SUP87-gal7			31	1	64	36.6	3.8	68
tsm7269-gal1			8	0	23	38.0	4.8	72
SUP87-SUP72			26	0	12	16.6	4.5	68
SUP87-lys2			33	1	40	31.4	5.1	68
SUP72-lys2			43	0	15	13.4	3.3	68
tsm7269-lys2			32	0	42	28.7	3.1	72
sec18-lys2			111	0	40	13.4	1.9	C. Fields, and R. Schekman, personal communication
sec18-tyr1			42	3	110	41.7	3.9	C. Fields and R. Schekman, personal communication
algl-lys2			45	0	2	2.2	1.5	33
ssn6-lys2			12	0	0	0		21
TEF2-lys2						2		162
glc6-lys2			117	0	16	6.2	1.6	J. Pringle, personal communication
SUP46-tyr1			685	1	140	8.8	0.7	143
sup47-lys2			74	1	59	24.4	3.1	143
syp47-tyr1			177	1	69	15.2	1.9	143
DUR80-tyr1			197	3	221	28.5	1.7	235
DUR80-dur1			390	0	31	3.8	0.7	235
DUR80-met8			404	0	17	2.1	.5	235

[a] See footnote *a*, Table 1, for abbreviations.

genes has been determined by cloning studies; two examples are the orders of *leu2-cen3-cdc10* (chromosome III) (28) and *cdc9-cdc39-ste7* (chromosome IV) (14, 149).

The genetic map is based mainly on data from tetrad analysis of the four meiotic products (ascospores) from individual diploid cells. For any given pair of heterozygous markers in a cross (AB × ab), tetrad dissection of the sporulated diploid will result in three types of asci: parental ditype (PD) (AB, AB, ab, ab), nonparental ditype (NPD) (Ab, Ab, aB, aB), and tetratype (T) (AB, Ab, aB, ab). Map distances are calculated by using the relative frequencies of these classes. In Tables 1 through 17 the map distances x' have been calculated with equations developed by R. Snow (173), using a maximum likelihood analysis. These equations give the most accurate determination of map distances since they take into account all classes of crossovers between two genes. These equations are very complex and require a computer to solve them. Although less accurate, most published map distances are calculated by using the equation derived by Perkins (7): $X_p = (100/2) \times [(T + 6NPD)/(PD + NPD + T)]$.

This equation is reasonably accurate for distances up to about 35 centimorgans (cM), but underestimates longer distances (for discussion of this, see references 111, 136, 173). An empirical formula has been developed which can be used to convert X_p (map distance calculated from Perkin's equation) into an accurate approximation of x' (111): $X_e = [(80.7\ X_p - 0.883\ X_p^2)/(83.3 - X_p)]$. X_e has been shown to be applicable for distances >35 cM and can be easily calculated. These mapping equations are used to determine whether two genes are linked and are applicable for distances up to approximately 100 cM.

There are many ways in which the general location of a gene can first be determined, and most of these techniques have recently been reviewed (131, 134). In the last few years additional techniques have been devised, including two new methods useful for mapping mutations. The *spo11* mapping method (89) is based on the analysis of the rare viable meiotic products resulting from meiosis of diploids homozygous for a recombination-deficient mutation. The *rad52* mapping method (D. Schild and R. K. Mortimer, Genetics, in press) is based on the high frequency of chromosome loss observed in diploids homozygous for the *rad52* mutation (128). This technique has also been modified to make it more suitable for mapping temperature-conditional mutations (P. J. Hanic-Joyce, Genetics, in press). Two new methods have also been developed to map cloned genes. The 2 μm mapping method (49) is based on the instability of a chromosome which contains an integrated plasmid containing part or all of 2 μm DNA (51). It is also now possible to map genes by using Southern hybridization to individual yeast chromosomes which are first separated with the new orthogonal-field-alternating gel electrophoresis (OFAGE) technique (19, 163; Carle and Olson, in press).

TABLE 3. New tetrad analysis data for chromosome III[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
SUP53-leu2			154	0	1	0.3	0.3	52
SUP53-leu2			90	1	3	4.8[b]		101
Total			244	1	4	1.2	0.9	
SUP53-cen3	75	19				10.7	2.4	101
Ty1-MAT			32	0	5	6.8	2.9	92
Ty1-thr4			23	0	23	25.1	3.7	92
sec55-MAT			67	2	100	33.3	3.1	C. Fields and R. Schekman, personal communication
sec55-thr4			139	0	26	7.9	1.4	C. Fields and R. Schekman, personal communication
SUF16-SUF2			285	0	25	4.1	0.8	55
SUF16-pgk1			233	0	4	0.9	0.4	55
SUF16-cen3	69	6				4.1	1.6	55
SUF16-pet18			56	0	6	4.9	1.9	55
SUF16-MAT			183	2	122	21.9	2.0	55
flk1-MAT			10	0	48	41.8	2.9	175
flk1-thr4			9	0	11	27.6	5.7	175
flk1-MAL2			40	0	16	14.8	3.4	175

[a] See footnote *a*, Table 1.
[b] X' could not be determined; calculated by Perkins' (7) equation for X_p.

GENETIC MAP, GLOSSARY, AND LIST OF MAPPED GENES

Edition 9 of the genetic map of *S. cerevisiae* is presented in Fig. 1. It is based on the data in Tables 1 through 17 and on data included in our previous review (132). A general discussion of the genetic map is included at the end of this article. The glossary (Table 18) briefly describes the phenotypes of different groups of genes. The chromosomal arm on which each mapped gene is located is included in the list of mapped genes (Table 19), as are one or more references which include data on the map position of the gene. More complete descriptions of each gene and the enzyme encoded by them, if known, have been presented by Plischke et al. (151) and Broach (15).

COMMENTS ON NEW ADDITIONS TO EACH CHROMOSOME

In this section, additions and changes to each of the chromosomes since our last major review (132) are discussed. Ambiguities in gene locations or orders are also discussed.

Chromosome I

FLO4 is an allele of *FLO1* and so has been removed from the map. The marker *osm*, which was placed on chromosome I by random spore analysis (176), has also been removed from the map due to lack of tetrad data. The mutation *cdc24* has been mapped on chromosome I distal to *cyc3* (85); it has also been shown to be allelic to *tsl1*, which has accordingly been removed from the map. Other genes added to chromosome I are *trn1* (G. Knapp, C. M. Cummins, and M. Culbertson, personal communication), *spo7* (R. E. Esposito and C. Waddell, personal communication), and *SUP56* (101). Chromosome I has been shown by OFAGE to have a size of 260 kilobases (kb) (Carle and Olson, in press). Its total genetic length is approximately 100 cM, which leads to a ratio of 2.6 kb/cM. By both criteria, chromosome I is the smallest yeast chromosome, with the possible exception of chromosome XVII (see Discussion).

Chromosome II

Chromosome II is one of the most densely mapped chromosomes, with 39 genes now distributed over its length of 250 cM. Since our last compilation (132), 15 genes have been added to chromosome II. *AMY2* and *cly2* have been shown to be on the left arm of this chromosome, with *AMY2* distal (199). The sporulation-deficient gene *spoT8* is on the right arm and distal to the *gal7,10,1* cluster (191). *SUP87*, a UGA suppressor (68), and *tsm7269* (72) map close to *tsm134*, and the order of these three genes and *pho3,5* relative to the centromere and each other is unknown. *sec18* (C. Fields and R. Schekman, personal communication), and *SUP72* (68) map distal to this cluster. The genes *alg1* (33) and *TEF2* (162) are very close together with the probable order *cen2-alg1-lys2-TEF2*. *ssn6* has been shown to be an allele of *cyc8* (21). *sup47* maps in the same region as the omnipotent suppressor *sup45* and these two genes are probably allelic; *SUP46*, another omnipotent suppressor, maps distal to these two genes (143). *dur2* and *DUR80* have been shown to be very close to *dur1* (25), and the distance of this cluster from *met8* has been shown to be much shorter than previously reported.

Chromosome III

Several changes have been made on chromosome III, the mating type chromosome. *SUP53* is now placed distal, rather than proximal, to *leu2* (52, 101) and *cdc10* is located on the right arm near the centromere rather than on the left arm (28). Two genes, *SUF16* and *sec55*, have been added to the map of this chromosome. The frameshift suppressor *SUF16* is 1 map unit distal to *pgk1* (55). The secretory mutant *sec55* maps 7.9 ± 1.4 cM distal to *thr4* (Fields and

TABLE 4. New tetrad analysis data for chromosome IV[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
SUF25-cdc9			181	6	230	32.2	2.2	55, 56
SUF25-trp1			42	22	114	110.2	38.6	55
SUF25-HO			176	0	66	13.7	1.5	56
cdc9-HO			80	14	148	53.7	7.7	56
cdc9-trp1			43	19	117	88.8	22.6	55
spoT4-trp1			33	2	53	37.7	5.9	191
spoT4-cdc7			24	0	26	26.8	4.1	191
PHS1-trp1			149	0	0	0		179
erg6-trp1			23	1	1	14.0[b]		122
tsm0080-cdc7			47	0	8	7.3	2.4	10; F. Boutelet and F. Hilger, personal communication
tsm0080-trp1			48	0	7	6.4	2.3	10; F. Boutelet and F. Hilger, personal communication
tsm0080-rad57			46	0	6	5.8	2.3	10; F. Boutelet and F. Hilger, personal communication
tsm0080-tsm5162			39	0	16	14.6	3.1	10; F. Boutelet and F. Hilger, personal communication
tsm5162-cdc7			33	0	22	20.1	3.3	10; F. Boutelet and F. Hilger, personal communication
tsm5162-trp1			34	0	21	19.1	3.3	10; F. Boutelet and F. Hilger, personal communication
cdc7-trp1			52	0	3	2.8	1.6	10; F. Boutelet and F. Hilger, personal communication
trp1-rad57			49	0	3	2.9	1.7	10; F. Boutelet and F. Hilger, personal communication
SUP88-trp1			37	0	17	15.8	3.2	68
SUP88-SUP80			20	0	34	32.0	3.6	68
SUP80-trp1			27	6	95	54.0	7.6	68
SUP80-nul3			22	2	41	42.1	8.3	68
ste5-aro1			6	0	3	17.0	8.5	166
ste5-hom2			4	0	9	34.8	6.7	166
sup36-aro1			17	1	19	35.1	10.8	143
sec1-hom2			112	0	6	2.6	1.0	C. Fields and R. Schekman, personal communication
sec1-sec5			115	0	3	1.3	0.8	C. Fields and R. Schekman, personal communication
sec5-cdc37			117	0	1	0.4	0.4	C. Fields and R. Schekman, personal communication
suf12-hom2			93	0	7	3.5	1.3	35
suf12-aro1			83	0	17	8.5	1.9	35
cdc37-aro1			44	0	17	14.0	2.9	166
cdc37-hom2			100	0	4	2.0	1.0	166
cdc37-ste5			8	0	11	29.1	5.8	166
adr1-aro1			12	2	25	51.5	16.2	J. Wood and C. L. Denis, personal communication
adr1-hom2			6	0	11	32.5	6.0	J. Wood and C. L. Denis, personal communication
adr1-pet14			34	0	2	2.8	2.0	J. Wood and C. L. Denis, personal communication
sec7-cdc37			113	0	5	2.2	1.0	C. Fields and R. Schekman, personal communication
sir4-hom2			20	7	55	72.0	20.7	J. M. Ivy, personal communication

Continued on following page

TABLE 4—*Continued*

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
sir4-lys4			56	0	26	16.2	2.8	J. M. Ivy, personal communication
hom2-lys4			19	10	54	104.9	48.8	J. M. Ivy, personal communication
rad9-pet14			22	0	9	14.6	4.2	E. L. Dowling, Ph.D. thesis
rad9-lys4			24	0	6	10.1	3.8	E. L. Dowling, Ph.D. thesis
pet14-lys4			19	0	10	17.3	4.5	E. L. Dowing, Ph.D. thesis
rad9-ade8			16	6	51	70.6	19.7	E. L. Dowling, Ph.D. thesis
SUF24-pet14			67	0	89	28.7	2.1	55
SUF24-lys4			115	0	44	14.0	1.9	55
SUF24-trp4			54	8	104	49.4	7.5	55
pet14-lys4			109	0	56	17.1	1.9	55
pet14-trp4			32	19	110	100.1	28.7	55
gcn2-lys4			55	2	42	28.1	5.7	73
gcn2-*pet14*			20	1	49	39.5	5.0	73
cdc40-lys4			56	11	112	56.1	9.4	Y. Kassir, M. Kupiec, A. Shalom, and G. Simchen, personal communication
cdc40-trp4			138	0	5	1.8	0.8	Y. Kassir, M. Kupiec, A. Shalom, and G. Simchen, personal communication
cdc40-ade8			29	5	59	52.5	11.1	Y. Kassir, M. Kupiec, A. Shalom, and G. Simchen, personal communication
pep7-lys4			15	2	41	47.2	9.0	E. Jones and M. Kolodny, personal communication
pep7-trp4			83	0	33	14.5	2.2	E. Jones and M. Kolodny, personal communication
pep7-ade8			46	5	60	44.3	9.4	E. Jones and M. Kolodny, personal communication
SUF3-trp4			124	0	53	15.1	1.8	56
SUF3-ade8			87	0	69	22.3	2.1	56
spt3-SUF3			49	0	1	1.0	1.0	205
spt3-trp4			14	0	9	19.7	5.2	205
spt3-ade8			53	0	37	20.9	2.8	205
cup14-ade8			68	3	73	32.4	4.6	J. Welch and S. Fogel, personal communication
cup14-trp4			42	8	106	53.2	7.8	J. Welch and S. Fogel, personal communication
snf1-rna3			87	0	11	5.6	1.6	22
snf1-ade8			32	2	59	38.8	5.5	22
pho8-ade8			218	13	157	33.1	4.4	86
pho8-rna3			213	1	35	8.3	1.8	86
snf1-ssn2			15	0	6	14.4	5.1	21

[a] See footnote *a*, Table 1.
[b] See footnote *b*, Table 3.

Schekman, personal communication), which places it very close to *mak14* (8.9 ± 2.9 cM distal to *thr4*). Two Ty1 sequences have been located on chromosome III, one distal to *leu2* and the other just distal to *pet18* (92). Finally, the marker *SAD1* was shown to be due to a structural change and not to a point mutation (87) and therefore has been removed from the map.

A circular chromosome resulting from an exchange between *HML* on the left arm and *MAT1* on the right arm has been isolated (178). This section has a genetic length of 81

TABLE 5. New tetrad analysis data for chromosome V[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
SUF19-can1			162	0	36	9.2	1.4	55
SUF19-mak10			141	0	11	3.6	1.1	55
SUF19-min1			209	0	5	1.2	0.5	55
rad23-ura3			45	0	11	9.9	2.7	123
rad23-cyc7			213	0	2	0.5	0.4	123
rad23-anp1			157	0	3	1.0	0.6	123
anp1-cyc7			20	0	1	2.5	2.8	123
anp1-ura3			138	1	44	13.8	2.4	123
cup5-can1			56	3	100	37.6	3.9	J. Welch and S. Fogel, personal communication
cup5-ura3			130	0	36	11.0	1.7	J. Welch and S. Fogel, personal communication
cup5-cen5	79	29				14.6	2.5	J. Welch and S. Fogel, personal communication
cup5-hom3			33	8	127	54.9	6.6	J. Welch and S. Fogel, personal communication
glc3-cen5	92	3				1.6	0.9	J. Pringle, personal communication
gcn4-ura3			45	0	9	8.4	2.6	73
SUP71-ura3			47	0	15	12.6	3.1	68
sec3-ura3			86	0	12	6.4	1.9	C. Fields and R. Schekman, personal communication
sec3-cen5	97	7				3.4	1.3	C. Fields and R. Schekman, personal communication
sec3-his1			22	3	69	47.5	6.6	C. Fields and R. Schekman, personal communication
tsm0039-ura3			52	0	9	7.4	2.3	10; F. Boutelet and F. Hilger, personal communication
tsm0039-cen5	61	0				0		10; F. Boutelet and F. Hilger, personal communication
tsm0039-arg9			61	0		0		10; F. Boutelet and F. Hilger, personal communication
GAL83-ura3			62	0	27	15.2	2.5	120
GAL83-arg9			80	0	9	5.1	1.6	120
gln3-gcn4			24	3	38	46.7	12.0	127
gln3-his1			48	0	11	9.8	3.0	127
gln3-arg6			37	0	15	14.5	3.2	127
gln3-trp2			22	0	30	28.9	3.5	127
NHS1-arg9			65	23	133	88.3	23.2	180
NHS1-hom3			610	1	9	1.4	1.0	180
NHS1-his1			562	2	41	4.5	1.0	180
NHS1-trp2			158	12	234	39.3	3.3	180
SUP85-his1			8	0	1	5.8	6.0	68
SUP85-SUP20			17	0	0	0		68
arg84-arg6			10	0	0	0		79
met6-ilv1			32	0	13	14.5	3.4	Schild and Mortimer, in press
met6-trp2			41	0	4	4.5	2.2	Schild and Mortimer, in press
pet-ts1402-ilv1			18	3	48	50.4	10.0	116
spt2-rad4			197	0	1	0.3	0.3	205

[a] See footnote *a*, Table 1.

cM. The isolated circular chromosome has a contour length of 62.6 μm, which corresponds to 180 kb. The ratio of physical size to genetic map length of this region of chromosome III is 2.2 kb/cM.

The whole of chromosome III has been resolved by OFAGE. The size of this chromosome is approximately 370 kb (19, 163; Carle and Olson, in press) and its total map length is 140 cM. Therefore, the ratio of physical size to genetic map length for all of this chromosome is 2.5 kb/cM.

Chromosome IV

Chromosome IV is the longest chromosome of yeast as determined by genetic mapping procedures (137). It is also one of the largest chromosomes as identified by OFAGE (19, 163; Carle and Olson, in press).

Since our last major review (137), 22 genes have been located on chromosome IV and several other changes have been made. The most distal gene on the left arm of this chromosome is a *SUC* gene (G. Kawasaki, Ph.D. thesis, University of Washington, Seattle, 1979) which has since been shown to be *SUC5* (20). *SUF25* has been located between *HO* and *cdc9* (55, 56), whereas the order, proximal to distal, of *cdc9*, *ste7*, and *cdc39* has been changed to *cdc9-cdc39-ste7* (14, 149). The sporulation-deficient gene *spoT4* maps distal to *mar1* on the left arm (94). Two genes, *PHS1* and *erg6*, map very close to *trp1* near the centomere of this chromosome (122, 179).

On the right arm, two temperature-sensitive lethals, *tsm0080* and *tsm5162*, and a UGA suppressor, *SUP88*, map distal but close to *trp1* (10, 68; F. Boutelet and F. Hilger, personal communication). Another UGA suppressor, *SUP80*, is further out on the right arm near *rad55* (68). The sterile mutation *ste5* maps 16.7 cM proximal to *aro1* (166) and has been shown to be allelic to *nul3* (J. Shuster, personal communication), which maps in the same location. The genes *sec1*, *sec5*, *cdc37*, and *sec7* are located in that order between 2.5 and 6.7 cM distal to *hom2* (166; Fields and Schekman, personal communication). *suf12* (55), as well as *sup35* (129) and *arg82* (72), map in the same region but these genes have not been tested for linkage against each other or against the *sec1-sec5-cdc37-sec7* group. The gene *adr1* is near *pet14* but the order of these two genes relative to the centromere is unknown (J. Wood and C. Denis, personal communication). *rad50* and *fol1*, which previously had been mapped to chromosome IV, have been found to map on

TABLE 6. New tetrad analysis data for chromosome VI[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
act1-cdc4			15	3	49	52.6	10.1	49
act1-tub2			22	0	0	0		J. Thomas, S. Falco, and D. Botstein, personal communication
tub2-cdc4			16	2	59	46.9	6.3	J. Thomas, S. Falco, and D. Botstein, personal communication
tsm0070-cdc4			19	0	13	20.4	4.4	10; F. Boutelet and F. Hilger, personal communcation
tsm0070-cen6	16	16				30.3	7.1	10; F. Boutelet and F. Hilger, personal communication
tsm0070-his2			13	2	17	53.6	26.4	10; F. Boutelet and F. Hilger, personal communication
sec4-cdc4			157	0	4	1.3	0.6	C. Fields and R. Schekman, personal communication
sec4-cen6	150	10				3.2	1.0	C. Fields and R. Schekman, personal communication
Ty1-his2			25	1	24	30.7	7.8	92
Ty1-cdc4			33	0	2	2.9	2.1	92
SUF20-cen6	252	24				4.5	0.9	55
SUF20-SUP11			265	0	7	1.3	0.5	55
SUF20-cly3			234	0	40	7.4	1.1	55
SUF20-SUF18			14	0	3	9.0	4.9	55
SUF18-cen6	165	67				15.8	1.8	55
SUF18-SUP11			41	0	9	9.1	2.8	55
SUF18-his2			31	0	15	16.4	3.5	55
SUF18-cly3			222	0	5	1.1	0.5	55
SUP57-his2			31	0	15	16.4	3.5	101
SUP57-met10			46	0	0	0		101
SUP57-SUP6			7	0	2	11.4	7.6	101

[a] See footnote *a*, Table 1.

chromosome XIV (93; J. Game, personal communication). The *rad* gene that was mapped on chromosome IV appeared spontaneously in a cross in which *rad50* was segregating and was incorrectly identified as this gene. *fol1* had previously been shown to be linked to *rad50* (J. Game and J. Little, personal communication). *rad9* and *sir4* map in the region between *pet14* and *lys4* (E. L. Dowling, Ph.D. thesis, University of California, Berkeley, 1982; J. M. Ivy, personal communication) but their relative order is unknown. Distal to *lys4* are *SUF24* (55) and *gcn2* (73). The former gene is a frameshift suppressor, whereas *gcn2* is involved in the control of general amino acid biosynthesis. *pep7* maps 14.5 cM proximal to *trp4* (E. Jones and M. Kolodny, personal communication), and close, but distal, to *trp4* is the cell cycle mutation *cdc40* (Y. Kassir, M. Kupiec, A. Shalom, and G. Simchen, personal communication), whereas further out on the right arm are *SUF3* (56) and *spt3* (205). The order of these two genes relative to *trp4* is unknown. Near the right terminus of this chromosome have been added *cup14* (J. Welch and S. Fogel, personal communication), *snf1* (22), *pho8* (86), and *ssn2* (21). The former gene is proximal to *rna3*; the other three are distal.

Chromosome V

Chromosome V was originally identified by the centromere-linked gene *ura3*. Since 1980, 13 additional genes have been located on this chromosome. *SUF19* maps between *min1* and *mak10* (55), but the position of *SUS1*, which maps in the same region, relative to these three genes has not been determined. *rad23* and *anp1* map close to *cyc7* (123). *cyc7* is one of two structural genes for cytochrome *c* synthesis and, interestingly, it has been pointed out (123) that the other gene, *cyc1*, which is on chromosome X, has close to it *rad7*, another excision-defective gene similar to *rad23*. The gene *cup5* maps between *anp1* and *ura3* (Welch and Fogel, personal communication). The following three genes have been mapped near the centromere of chromosome V: *glc3* (J. Pringle, personal communication), *gcn4* (73), and *sec3* (Fields and Schekman, personal communication). *mnn1* and *SUP71* had already been mapped in this region. *mnn1* failed to recombine with the centromere in 41 tetrads, whereas *SUP71* is 2.5 cM from the centromere on the right arm (130). *glc3* is 1.6 cM from the centromere, *sec3* is 3.4 cM from the centromere and on the right arm, and *gcn4* is 8.4 cM from *ura3*, which would place it near the centromere (*ura3* is 8.0 cM from the centromere). None of these five genes has been tested for linkage against each other, so their order relative to each other or the centromere is unknown.

gln3 is 9.8 cM proximal to *his1* (127) and the gene *NHS1*, which is involved in H_2S production, is 1.4 cM proximal to *hom3*; this places it very close to *BOR1* (180). *SUP85* maps distal to *his1* (68) and fails to recombine with *SUP19,20*, which also have been mapped in this region. *arg84* fails to recombine with *arg6*; it is believed to be a mutation in the promoter region of the *arg5 arg6* gene complex (79).

In previous editions of the map, *met5* was placed between *trp2* and *rad51* (132). We have now shown that this gene is *met6* and that *met5* maps on the right arm of chromosome X (Schild and Mortimer, in press). *eth2* (*sam2*) had been shown to be linked to *met6*, so it has been assigned to chromosome V as well. It is provisionally placed distal to *met6* but it could also be proximal. A temperature-sensitive genetic petite, *pet-ts1402*, maps 50 cM distal to *ilv1* (116). *spt2* is less than a map unit from *rad4*, located much further out on the right arm of this chromosome (205). Recent data place *rad24* (r_1^s) distal to *rad3* (Game, personal communication).

Chromosome VI

Chromosome VI is one of the shortest in genetic map length. It is also the second smallest chromosome as determined by OFAGE (Carle and Olson, in press). Its map length

TABLE 7. New tetrad analysis data for chromosome VII[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
spoT2-ade5			27	0	7	10.4	3.6	M. Tsuboi, personal communication
spoT2-lys5			12	2	26	51.3	15.5	M. Tsuboi, personal communication
rad54-lys5			43	0	15	13.0	2.9	E. L. Dowling, Ph.D. thesis
rad54-met13			42	0	39	24.4	3.0	E. L. Dowling, Ph.D thesis
cup2-lys5			82	0	12	6.4	1.7	J. Welch and S. Fogel, personal communication
cup2-aro2			77	1	34	18.1	3.7	J. Welch and S. Fogel, personal communication
cup2-met13			34	1	54	33.9	4.2	J. Welch and S. Fogel, personal communication
SUP38-ade5			5	2	13	NL		B. Ono, personal communication
SUP38-lys5			10	0	13	29.5	6.4	B. Ono, personal communication
SUP38-cyh2			20	0	2	4.7	3.4	B. Ono, personal communication
mfα2-lys5			47	6	92	46.7	6.9	S. Caplan and J. Kurjan, personal communication
mfα2-aro2			49	5	87	43.4	6.3	S. Caplan and J. Kurjan, personal communication
mfα2-met13			86	1	52	21.0	3.0	S. Caplan and J. Kurjan, personal communication
mfα2-cyh2			206	1	26	7.0	1.9	S. Caplan and J. Kurjan, personal communication
mfα2-trp5			6	1	17	50.2	16.2	S. Caplan and J. Kurjan, personal communication
hem10-leu1			9	0	8	23.7	6.3	193
hem10-ole1						3.3		D. Urban-Grimal and R. Labbe-Bois[b]
hem10-trp5						14.0		D. Urban-Grimal and R. Labbe-Bois[b]
SUP54-trp5			44	0	6	6.1	2.4	101
SUP54-leu1			29	0	22	21.6	3.5	101
SUP54-cen7	24	17				24.0	5.4	101
ate1-leu1			46	0	2	2.1	1.5	160
ate1-trp5			31	0	6	8.2	3.1	160
smr2-cen7	101	22				9.4	1.9	50
smr2-cyh3			24	0	0	0		50
tsm0119-ant1			78	0	6	3.6	1.4	10; F. Boutelet and F. Hilger, personal communication
tsm0119-leu1			81	0	3	1.8	1.1	10; F. Boutelet and F. Hilger, personal communication
ant1-leu1			79	0	5	3.0	1.3	29
Ty1-leu1			88	0	21	9.9	2.1	92
rme1-trp5			25	0	35	29.6	3.5	156
rme1-leu1			44	0	16	13.4	2.9	156
rme1-ade6			39	0	19	16.9	3.5	156
sup112-trp5			18	2	38	44.8	9.3	B. Ono, personal communication
sup112-ade6			73	0	15	8.6	2.0	B. Ono, personal communication
alg7-trp5			24	1	18	29.1	9.6	6
alg7-cly8			8	0	12	30.1	5.6	6
cdc62-leu1			5	0	32	43.3	2.9	P. J. Hanic-Joyce, in press
cdc62-ade6			27	1	12	24.6	12.1	P. J. Hanic-Joyce, in press
ade6-cly8			28	3	58	44.3	7.4	23
ade6-SUF4			20	8	61	75.5	21.1	23
cly8-SUF4			48	2	39	29.7	6.4	23
SUF4-ser2			57	21	161	73.8	12.6	38
SUF4-ade3			69	17	172	60.0	8.1	38
SUF15-ser2			160	0	18	5.1	1.1	55
SUF15-ade3			142	0	30	8.9	1.5	55
ser2-ade3			159	0	11	3.3	1.0	55
hip1-ade3						10.8		J. Tanaka and G. R. Fink[c]
SUP76-ade3			20	0	17	23.0	4.2	68
SUF76-SUP77			22	0	25	27.2	4.1	68
SUP77-ade3			5	7	25	NL[d]		68

[a] See footnote *a*, Table 1.
[b] Abstr. Int. Conf. Yeast Genet. Mol. Biol, 11th, p.87, 1982.
[c] Abstr. Mol. Biol. Yeast Meet., Cold Spring Harbor, N.Y., 1983.
[d] NL, Not linked.

and physical size are 140 cM and 290 kb, respectively. Our first review positioned 13 genes along this chromosome; 8 genes have been added since. The structural genes for actin and β-tubulin, which fail to recombine, are now the distalmost markers on the left arm and are located about 50 cM from *cdc4* (49; J. Thomas, S. Falco, and D. Botstein, personal communication). These genes have been shown to be separated by approximately 1.5 kb of DNA. In the region between these two genes is a sequence with close homology to the human *ras has/bas* oncogene (57). *tsm0070* maps 20.4 ± 4.4 cM distal to *cdc4* (10; F. Boutelet and F. Hilger, personal communication), which places it close to *SUF9* which in turn is 16.5 ± 5.7 cM distal to the same gene (136). *sec4* is about 1 map unit proximal to *cdc4* (Fields and Schekman, personal communication), whereas a Ty1 element is 3 cM proximal to the same gene (92). *SUF20* maps between *SUP11* and the centromere on the right arm, whereas *SUF18* is 1.1 cM proximal to *cly3* further out on this chromosome arm (55). *SUP57*, a UAG suppressor, fails to recombine with *met10*; this places it very close to *SUP6*

TABLE 8. New tetrad analysis data for chromosome VIII[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
dur3-spo11			186	1	62	13.7	1.9	T. Cooper and M. Mojumdar, personal communication
dur3-cen8	144	105				24.5	2.2	T. Cooper and M. Mojumdar, personal communication
dur3-arg4			129	3	117	27.4	2.7	T. Cooper and M. Mojumdar, personal communication
dur3-dur4						0.4		T. Cooper and M. Mojumdar, personal communication
spo11-cen8	98	151				39.8	3.3	T. Cooper and M. Mojumdar, personal communication
spo11-arg4			90	4	155	36.3	2.9	T. Cooper and M. Mojumdar, personal communication
ard1-arg4			52	0	1	1.0	1.1	M. Whiteway and J. Szostak, personal communication
ard1-cen8	49	25				18.9	3.5	T. Cooper and M. Mojumdar, personal communication
tsm0186-arg4			39	0	5	5.7	2.5	10; F. Boutelet and F. Hilger, personal communication
tsm0186-thr1			39	0	5	5.7	2.5	10; F. Boutelet and F. Hilger, personal communication
tsm0151-arg4			37	0	7	8.0	2.8	10; F. Boutelet and F. Hilger, personal communication
tsm0151-thr1			42	0	2	2.3	1.7	10; F. Boutelet and F. Hilger, personal communication
tsm0151-tsm0186			40	0	4	4.6	2.3	10; F. Boutelet and F. Hilger, personal communication
put2-arg4			31	1	21	26.3	7.7	11
put2-thr1			40	0	11	10.8	2.9	11
put2-CUP1			41	1	10	17.4	10.4	11
sup111-arg4			31	2	52	38.4	6.1	B. Ono, personal communication
sup111-thr1			23	0	24	26.1	4.1	B. Ono, personal communication
spo12-pet3			75	0	0	0		89

[a] See footnote *a*, Table 1.

(approximately 2 cM from *met10*), although these two suppressors recombine (101).

Chromosome VII

Chromosome VII one of the largest yeast chromosomes; only IV and XII are larger and XV is near the same size (Carle and Olson, in press). Until recently, the genetic map length of this chromosome was uncertain because a group of genes had been placed on the right arm only by mitotic crossing-over procedures (157). These studies indicated that *MAL1/SUC1* were the most proximal genes of this group. It has recently been shown that *SUF4*, which was the most "distal" mapped gene relative to *MAL1/SUC1*, is in fact proximal to *MAL1/SUC1* and linked to *cly8* (23), which is about 45 cM from the centromere (130). Thus, this group of genes from *MAL1/SUC1* to *SUF4* has been reversed, placing *MAL1/SUC1* as the most distal genes on the right arm. There is evidence that *SUC1* is the distal-most marker and is adjacent to the telomere on the right arm of chromosome VII (J. Celenza and M. Carlson, personal communication). This is remarkable in that all other mapped fermentation genes (reviewed in reference 132) and many of the glycolytic genes (109, 114, 115; Z. Lobo, Ph.D. thesis, University of Bombay, Bombay, India, 1976) are also on or near the ends of chromosomes.

On the left arm, *ade5* has been changed to *ade5,7* (157) and *spoT2* has been shown to map proximal to this gene (191). *rad54* (E. L. Dowling, Ph.D. thesis), *cup2* (Welch and Fogel, personal communication), and *cdc43* (A. Adams and J. Pringle, personal communication) map distal to *lys5* but the order of these genes relative to *lys5* and *ski1* is unknown. *sup38* maps distal to *cyh2* (B. Ono, personal communication), whereas the structural gene for the α mating type factor, *mfα2*, maps 7.0 cM proximal to this gene (S. Caplan and J. Kurjan, personal communication). The gene *hem10* is 3.3 cM from *ole1* (Urban-Grimal, personal communication), but its order relative to *rad6*, which maps in the same region, is uncertain. *SUP54* maps 6.1 cM from *trp5* (101) and is probably distal to this gene, whereas *ate1* is 2 cM from *leu1*, also probably distal (160). *tsm0119* is also near *leu1* (Boutelet

TABLE 9. New tetrad analysis data for chromosome IX[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
rev7-SUC2			2	10	30	NL[b]		C. W. Lawrence, personal communication
rev7-SUC2			11	0	14	28.1	5.1	C. W. Lawrence, personal communication
Total			13	10	44	NL		
rev7-his5			84	0	27	12.2	2.1	C. W. Lawrence, personal communication
rev7-lys11			24	3	41	46.5	11.0	C. W. Lawrence, personal communication
lys11-his5			16	1	27	38.2	8.4	C. W. Lawrence, personal communication
tsm0139-lys11			28	1	26	29.7	7.1	10; F. Boutlet and F. Hilger, personal communication
tsm0139-his6			14	1	17	37.6	12.7	10; F. Boutlet and F. Hilger, personal communication
dal81-his6			69	10	126	49.2	6.9	192
dal81-dal1			181	2	22	9.2	3.6	192
dal81-dal4			172	1	32	9.4	2.1	192

[a] See footnote *a*, Table 1.
[b] NL, Not linked.

TABLE 10. New tetrad analysis data for chromosome X[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
eam1-ino1			50	0	11	9.1	2.5	3
ino1-cdc6			81	0	63	21.9	2.1	42
ino1-ura2			120	0	29	9.9	1.7	42
ino1-arg3			14	1	31	40.8	7.7	42
arg3-SUP7			24	0	37	30.8	3.4	72
arg3-ura2			49	0	48	25.0	2.7	72
arg3-cdc6			29	8	82	61.6	11.9	72
ura2-SUP7			7	2	44	54.4	9.3	72
ura2-cdc6			27	0	38	29.6	3.3	72
SUP74-SUP7			6	0	0	0		68
SUP74-SUP73			35	0	9	10.3	3.1	68
SUP73-SUP51			13	0	7	17.6	5.5	68
cyr1-cen10	52	3				2.8	1.6	121
cyr1-ilv3			62	0	18	11.6	2.6	121
tsm0185-cen10	35	8				9.8	3.3	10; F. Boutelet and F. Hilger, personal communication
tsm0185-met3			43	0	1	1.2	1.3	10; F. Boutelet and F. Hilger, personal communication
tsm0185-ilv3			41	0	3	3.5	2.1	10; F. Boutelet and F. Hilger, personal communication
rev5-met3			7	0	14	33.5	5.3	C. W. Lawrence, personal communication
rev5-ilv3			10	0	7	20.8	6.2	C. W. Lawrence, personal communication
rev5-cyc1			18	0	1	2.8	3.0	C. W. Lawrence, personal communication
rev5-cdc8			68	0	9	5.9	1.9	C. W. Lawrence, personal communication
SUF23-cyc1			589	0	22	1.8	0.4	56
SUF23-rad7			266	0	0	0		56
SUF23-SUP4			186	0	9	2.3	0.8	55
SUF23-cdc11			504	4	250	18.1	1.2	55, 56
met5-cdc11			9	0	13	29.7	5.4	Schild and Mortimer, in press
hom6-cdc11			32	2	48	37.5	6.5	Schild and Mortimer, in press
met5-hom6			63	0	5	3.7	1.6	Schild and Mortimer, in press

[a] See footnote *a*, Table 1.

and Hilger, personal communication). There are now nine genes that map very close to *leu1*; most of these genes confer resistance to drugs (*BOR2*, borrelidin; *cyh3* cycloheximide; *til1*, thiaisoleucine; *ant1*, antibiotic; *AMY1*, antimycin; *oli1*, oligomycin; *AXE1*, axenomycin). It has been proposed that these genes are alleles or are part of a genetic complex coding for ribosomal proteins (159). *smr2*, a mutation that confers resistance to the herbicide sulfometuron methyl, fails to recombine with *cyh3* (50).

A transposable element, Ty1, is on the right arm about 10 cM from *leu1* (92), and *rme1*, which is possibly an allele of *dsm1* (156), is 13.4 cM from *leu1*. *alg7* shows linkage to *trp5* and *cly8* and appears to map in the region between *ade6* and the centromere (6). *sup112* maps 8.6 cM distal to *ade6* (Ono, personal communication) and *cdc62* is near *cly8* but its position relative to *ade6* is unknown (Hanic-Joyce, in press). The genes *SUF4* (56), *SUP77* (68), *SUP76* (68), and *hip1* (J. Tanaka and G. R. Fink, Abstr. Mol. Biol. Yeast Meet., p. 284, 1983) had all been mapped distal to *ade3*, but, as discussed above, they are now proximal. *hip1* also is linked to *ade3* but it is not known if it is proximal or distal to this gene (Tanaka and Fink, Abstr. Mol. Biol. Yeast Meet., 1983). As mentioned earlier, *SUF4*, formerly the most distal of this group, maps only 29 cM from the proximal marker

TABLE 11. New tetrad analysis data for chromosome XI[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
SUP33-fas1			101	0	13	5.7	1.5	B. Ono, personal communication
SUP33-trp3			122	0	106	23.4	1.7	B. Ono, personal communication
lap1-mak9			25	1	13	26.3	12.0	190
lap1-fas1			132	0	24	7.9	1.6	190
lap1-lap4			25	0	9	13.3	3.9	190
lap1-ura1			29	5	103	50.1	6.0	190
lap1-trp3			23	4	77	50.4	7.2	190
lap4-mak9			6	1	10	53.3	30.5	190
lap4-fas1			8	0	9	26.6	6.3	190
SUP75-trp3			5	1	14	53.5	21.0	D. Hawthorne, personal communication
SUP75-ura1			10	1	25	44.0	10.0	D. Hawthorne, personal communication
SUP75-met14			11	6	21	NL[b]		D. Hawthorne, personal communication
SUP58-cen11	19	33				42.8	7.5	101
SUP58-met14			20	3	30	51.3	17.0	101
SUP58-met1			10	7	32	144.8	145.9	101
gcn3-met14			95	0	10	4.8	1.5	156
dal80-cdc16			104	1	66	21.1	2.6	192
dal80-met14			127	0	44	13.0	1.8	192
dal80-met1			52	4	115	41.4	4.2	192
spoT23-met14			59	0	35	18.6	2.5	191
spoT23-met1			19	0	39	34.1	3.4	191
spo14-cdc16			9	0	15	31.4	5.1	M. Townsend, B. diDomenico, S. Klapholz, and R. Esposito, personal communication
spo14-met14			28	0	20	20.9	3.6	M. Townsend, B. diDomenico, S. Klapholz, and R. Esposito, personal communication
met20-met1			175	0	2	0.6	0.4	119
sir1-met1			31	1	35	31.0	5.7	J. M. Ivy, personal communication
sir1-met14			7	2	59	53.1	6.8	J. M. Ivy, personal communication
sir1-mak15			30	1	19	26.0	8.3	J. M. Ivy, personal communication
sir1-MAL4			52	0	0	0		J. M. Ivy, personal communication
SUP-1A-met1			18	2	56	45.6	6.5	17
SUP-1A-MAL4			74	0	0	0		17

[a] See footnote *a*, Table 1.
[b] NL, Not linked.

cly8. *SUF15* (55) and *fol2* (J. Game, J. Little, and B. Rockmill, personal communication) also have been located in the *SUF4-SUC1/MAL1* interval.

Chromosome VIII

Chromosomes VIII and V, which are about the same size (580 kb), are in the group of medium-sized chromosomes as determined by OFAGE (Carle and Olson, in press). The meiotic length of the region between *mak7* (distal-most on the left arm) and *mak19* (distal-most on the right arm) has been determined by collective tetrad analyses to be about 180 cM. *mak20* had been assigned to chromosome VIII by trisomic analyses and to the left arm because of a lack of mitotic linkage to right arm markers (198). Although trisomic analysis has been used successfully to map many genes, it is not always reliable. In view of this, the assignment of *mak20* to this chromosome must be considered provisional. The genes *dur3* and *dur4*, which fail to recombine, map 24.5 cM from the centromere and 13.7 cM distal to *spo11* on the left arm (T. Cooper and M. Mojumdar, personal communication). On the right arm, *ard1* is 1 cM proximal to *arg4* (M. Whiteway and J. Szostak, personal communication), and *spo13* has now been shown to be proximal, rather than distal, to *arg4* (S. Klapholz and R. E. Esposito, personal communication). Two temperature-sensitive lethals, *tsm0186* and *tsm0151* map in the *arg4-thr1* interval (F. Boutelet and F. Hilger, personal communication). *put2* is 2.9 cM distal to *thr4* (11) and *sup111* appears to map close to *CUP1* (Ono, personal communication) but its position, proximal or distal, to this gene is unknown. *spo12* fails to recombine with *pet3* and, in addition, the order of *SUF8* and *pet3* on this chromosome has been reversed (89). Finally,

TABLE 12. New tetrad analysis data for chromosome XII[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
ppr1-cen12	55	8				6.6	2.2	104
ppr1-asp5			54	0	9	7.2	2.3	104
SUP37-asp5			8	2	18	62.4	28.3	B. Ono, personal communication
SUP37-gal2			12	1	23	41.4	10.3	B. Ono, personal communication
pep3-gal2			71	9	192	46.6	4.1	206
pep3-RDN1			218	1	53	10.9	1.7	206
gal2-RDN1			61	17	194	60.0	7.0	206
ilv5-RDN1			19	5	22	118.5	181.8	148
ilv5-ura4			48	10	82	60.8	13.9	148
ilv5-car2			12	6	34	98.5	52.7	148
ura4-car2			23	0	21	24.5	4.3	148
nam2-ura4			18	0	13	21.1	4.5	46
SUP86-ura4			24	0	0	0		68
cup3-ura4			86	2	37	20.4	4.8	J. Welch and S. Fogel, personal communication
cup3-car2			14	0	6	15.1	5.3	J. Welch and S. Fogel, personal communication
mar2-ura4			29	0	48	31.5	3.0	A. Klar, personal communication
mar2(ste8)-ura4			26	2	29	38.3	10.7	R. K. Chan, personal communication
Total			55	2	77	33.5	3.9	
sst2-ura4			14	1	12	36.4	17.6	R. K. Chan, personal communication
sst2-mar2(ste8)			23	0	4	7.5	3.6	R. K. Chan, personal communication

[a] See footnote *a*, Table 1.

Celenza and Carlson (personal communication) have determined by the *spo11* mapping method that *SUC7* is on chromosome VIII but have not localized the gene on this chromosome.

Chromosome IX

There have been relatively few changes on chromosome IX since our last review. Chromosome IX is the fourth smallest chromosome (460 kb) as determined by OFAGE (Carle and Olson, in press) and it is still rather sparsely populated with genes. *rev7* has been mapped against *SUC2*, *his5*, and *lys11*, genes already located on the left arm, and appears to be located close to *SUP22* (C. Lawrence, personal communication). Since *rev7* has not been mapped against this suppressor, the order of these two genes relative to outside markers is unknown. The temperature-sensitive lethal *tsm0139* maps between *lys11* and *his6* (Boutelet and Hilger, personal communication) and is probably located proximal to *SUP17*. Finally, two genes have been added to the *dal* complex on the right arm; *dal81*, a regulatory site, maps proximal to the complex, whereas *dal3* maps distal (192).

Chromosome X

In order of increasing physical size, chromosome X ranks seventh (Carle and Olson, in press). Its genetic map length from *cdc6* on the left arm to *hom6* on the right arm is approximately 200 cM. The killer maintenance gene *mak17* has been mapped as the distal-most gene on the left arm by mitotic crossing-over procedures (198). It fails to show meiotic linkage to *ura2* but has not yet been tested for meiotic linkage to *cdc6* which is more distal. The genes *eam1* (3) and *ino1* (42) map between *cdc6* and *ura2* but their order, relative to these two flanking markers, is unknown. *arg3* maps in the *ura2-SUP7* interval about midway between these two genes (72). *SUP74*, a UGA suppressor, fails to recombine with *SUP7*, an ochre suppressor (68). It seems unlikely that these suppressors are alleles; *SUP7* is a tyrosine-inserting ochre suppressor and it is improbable that a gene coding for $tRNA^{Tyr}$ could mutate to recognize a UGA codon. *SUP73*, another UGA suppressor, maps 10.3 cM proximal to *SUP74* (68). *cyr1* defines the adenylate cyclase gene (121) and *tsm0185*, which maps in the same region and is allelic with *cdc35*, is deficient in adenylate cyclase activity (Boutelet and Hilger, personal communication). *rev5* (Lawrence, personal communication) and *SUF23* (55, 56) have been added to the cluster of genes that map very close to *cyc1*, the structural gene of iso-1-cytochrome *c*. *rev5* appears to be the most proximal of this group and *SUF23* failed to recombine in 266 tetrads with *rad7*, which is also in this group (55, 56). Two new genes have been added to the distal region of the right arm of chromosome X. *met5* and *hom6*, which are only 3.6 cM apart, map 37.5 cM distal to *cdc11* (Schild and Mortimer, in press). The preferred order of these two genes places *met5* proximal, but this is still uncertain.

Chromosome XI

Chromosome XI is unusual in that a large group of linked genes, extending from *mak9* to *cly7*, has been located on this chromosome only by trisomic analyses, and this association, at least for *ura1* which is part of this group, has been known for at least 25 years. Remarkably, no meiotic linkage be-

TABLE 13. New tetrad analysis data for chromosome XIII[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
GAL80-rad52			95	1	45	18.2	3.0	Schild and Mortimer, in press
GAL80-SUP79			20	0	23	26.8	3.8	Schild and Mortimer, in press
rad52-SUP5			18	0	13	21.1	4.5	Schild and Mortimer, in press
GAL80-SUP5			11	0	0	0		Schild and Mortimer, in press
SUP79-rad52			16	0	6	13.8	4.9	68
SUP79-rad52			12	1	30	42.5	8.2	Schild and Mortimer, in press
Total			28	1	36	32.7	5.8	
SUF22-SUF7			165	0	9	2.6	0.9	55
SUF22-cen13	74	103				37.4	3.6	55
SUF7-cen13	79	98				34.8	3.3	55
tsm0111-cen13	26	1				1.9	1.9	10; F. Boutelet and F. Hilger, personal communication
tsm0111-tsm0800			43	0	9	8.7	2.7	10; F. Boutelet and F. Hilger, personal communication
tsm0111-arg80			18	0	22	28.2	4.5	10; F. Boutelet and F. Hilger, personal communication
tsm0800-cen13	90	25				11.6	2.2	10; F. Boutelet and F. Hilger, personal communication
tsm0800-arg80			79	0	34	15.3	2.3	10; F. Boutelet and F. Hilger, personal communication
sec59-rad52			58	0	71	27.7	2.3	C. Fields and R. Schekman, personal communication
sec59-cen13	100	8				3.8	1.4	C. Fields and R. Schekman, personal communication
rad52-cen13	61	44				24.3	3.4	C. Fields and R. Schekman, personal communication
spoT1-cen13	224	0				0		M. Tsuboi, personal communication
spoT1-lys7			14	1	22	38.9	10.3	M. Tsuboi, personal communication
spoT1-cdc5			13	0	6	15.9	5.5	M. Tsuboi, personal communication
mcm1-lys7						2		G. Maine and B. Tye, personal communication
adh3-lys7						16		M. Ciriacy, personal communication
SMR1-ilv2			31	0	0	0		50
SMR1-lys7			39	1	44	30.0	4.6	50
pet-ts2858-ilv2			35	1	18	23.2	7.8	116
pet-ts2858-rna1			14	4	33	66.9	23.9	116
ilv2-rna1			12	5	39	75.2	25.7	D. Hawthorne, personal communication
sup113-cen13	11	27			Unlinked			B. Ono, personal communication
sup113-lys7			21	0	15	20.9	4.2	B. Ono, personal communication
ilv2-lys7			82	5	119	37.1	4.1	148
ilv2-lys7			14	1	41	42.3	6.1	D. Hawthorne, personal communication
Total			96	6	160	38.2	3.4	
ilv2-arg80			9	0	10	26.5	5.9	148
SUP78-SUP8			5	0	8	31.0	7.1	68
spoT7-rna1			245	0	6	1.2	0.5	M. Tsuboi, personal communication
spoT7-mak27			118	0	20	7.3	1.5	M. Tsuboi, personal communication
prc1-rna1			36	8	113	54.8	7.5	E. Jones, M. Aynardi, and M. Kolodny, personal communication
prc1-SUP8			79	0	30	14.0	2.3	E. Jones, M. Aynardi, and M. Kolodny, personal communication
ade4-rna1			19	1	49	40.1	5.1	Schild and Mortimer, in press
ade4-SUP8			16	0	11	20.5	4.8	Schild and Mortimer, in press
cdc61-rna1			18	1	21	34.8	9.8	Hanic-Joyce, in press
cdc61-ade4			15	0	26	31.8	3.8	Hanic-Joyce, in press

[a] See footnote *a*, Table 1.

TABLE 14. New tetrad analysis data for chromosome XIV[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
SUF6-pha2			88	9	98	43.4	7.6	56
SUF6-met2			185	0	15	3.8	0.9	56
SUF6-pet2			147	1	52	14.6	2.2	56
sec2-pha2			58	5	126	42.2	4.3	C. Fields and R. Schekman, personal communication
sec2-met2			148	0	37	10.2	1.6	C. Fields and R. Schekman, personal communication
rad50-pha2			12	1	35	43.2	7.2	93
rad50-met2			99	0	33	12.5	1.9	93
rad50-met2			13	0	5	14.0	5.5	J. Game, personal communication
Total			112	0	38	12.7	1.8	
rad50-pet2			173	0	23	5.9	1.2	93
rad50-pet2			13	0	0	0		J. Game, personal communication
Total			186	0	23	5.5	1.1	
rad50-petx			26	0	21	22.4	3.7	93
fol1-pet2			13	0	0	0		J. Game, personal communication
fol1-rad50			29	0	0	0		J. Game, personal communication
suf14-pet2			77	7	124	41.7	5.0	35
suf14-petx			81	0	25	12.1	2.2	35
suf14-mei4			115	15	261	46.9	3.9	35
met4-pet2			43	22	137	91.0	21.0	35
met4-petx			27	8	70	66.0	15.4	35
leu4-met4			21	0	0	0		Chang et al., in press
pms1-met4			32	0	11	12.9	3.4	Williamson et al., in press
pms1-top2			39	0	4	4.7	2.3	Williamson et al., in press
top2-met4			36	0	7	8.2	2.9	Williamson et al., in press
top2-met4			90	1	35	16.5	3.3	K. Voelker, S. DiNardo, and R. Sternglanz, personal communication
total			126	1	42	14.3	2.5	
top2-pet8			38	4	84	44.2	5.9	K. Voelker, S. DiNardo, and R. Sternglanz, personal communication
RAS^{sc}2-met4			26	0	1	2.0	2.2	88
RAS^{sc}2-met4			90	0	7	3.6	1.3	L. Robinson and K. Tatchell, personal communication
Total			116	0	8	3.2	1.1	
RAS^{sc}2-pet8			25	7	65	63.7	14.8	L. Robinson and K. Tatchell, personal communication
met4-pet8			48	20	151	76.5	13.7	90
met4-pet8			24	4	57	50.8	9.9	199
met4-pet8			5	2	11	95.9	95.4	88
met4-pet8			22	10	94	70.3	13.3	K. Voelker, S. DiNardo, and R. Sternglanz, personal communication
met4-pet8			24	7	66	64.0	14.6	L. Robinson and K. Tatchell, personal communication
Total			123	43	379	68.5	6.8	

Continued on following page

TABLE 14—*Continued*

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
spo1-pet8			107	0	9	3.9	1.3	90; B. diDomenico and R. Esposito, personal communication
spo1-rna2			32	0	7	9.0	3.2	90; B. diDomenico and R. Esposito, personal communication
pet8-rna2			35	0	5	6.3	2.7	90; B. diDomenico and R. Esposito, personal communication
$Tyl_a Tyl_b$			88	0	7	3.7	1.4	92
Tyl_a-*pet8*			16	0	8	16.8	5.0	92
Tyl_b-*met4*			20	3	40	49.5	12.0	92
Tyl_b-*pet8*			28	0	16	18.2	3.7	92
Tyl_b-*lys9*			33	2	54	37.8	5.9	92
pet494-rna2			62	3	123	37.8	3.3	138
pet494-lys9			273	0	14	2.4	0.6	138
SUP28-pet8			25	1	66	39.3	3.9	B. Ono, personal communication
SUP28-lys9			86	0	12	6.2	1.7	B. Ono, personal communication
hol1-lys9						4.7		P. Farabaugh, personal communication

[a] See footnote *a*, Table 1.

tween any of these genes and other chromosome XI markers has as yet been detected. Very recently, B. Glassner and R. K. Mortimer (personal communication) have shown mitotic linkage between *cdc16* and *ura1*. Added to this group of orphaned genes since our last review (132) are *SUP33* near *fas1* (Ono, personal communication), *lap1* and *lap4* (190), located between *fas1* and *mnn4*, and *SUP75*, near *cly7* (D. Hawthorne, personal communication).

SUP58 shows meiotic linkage to *met14*, located near the centromere of this chromosome, and is the proximal-most marker on the left arm (101). On the right arm, *gcn3* is 4.8 cM distal to *met14* (73) and *dal80* maps 13.0 cM distal to *met14* (192). Near *dal80* are *spo14* (M. Townsend, B. di Domenico, S. Klapholz, and R. E. Esposito, personal communication) and *spoT23* (191), which map in the same region; these two sporulation genes may be allelic. The gene *met20* maps about 0.5 cM from *met1* (119), and *sir1* was mapped by the integrated plasmid method and shown to be very close to *MAL4* (J. M. Ivy, personal communication). A cloned DNA fragment that behaves as an amber suppressor, *SUP-1A*, when present in high copy number, also fails to recombine with *MAL4* (17).

Chromosome XII

Chromosome XII is very likely the largest of the yeast chromosomes. Its meiotic length from *mak12* on the left arm to *car2* on the right arm is approximately 300 cM. In addition, this chromosome carries about 120 copies of the rDNA genes of yeasts (150); each copy has 9.1 kb of DNA. As yet unexplained is the observation that meiotic recombination in the rDNA region is only about 1% of that expected on the basis of the amount of DNA (150). If we were to assume normal recombination frequencies in this region (ca. 0.3 cM/kb), chromosome XII would have a recombination length of approximately 630 cM. This would make it genetically larger than chromosome IV, which has a recombination length of about 500 cM. It is interesting that during OFAGE analysis chromosome XII frequently failed to leave the sample well, and when it did, it left in a fashion suggesting to the authors that its movement was restricted by factors (e.g., nucleolus) other than those governing normal DNA migration (Carle and Olson, in press). Our analysis indicates that chromosome XII probably is the largest yeast chromosome and suggests that perhaps only the physical size of this chromosome determines its migration behavior.

Nine genes have been added to this chromosome since our last review. These include *ppr1*, which maps between the centromere and *asp5* on the right arm (104), and *SUP37* (Ono, personal communication) and *pep3* (E. Jones, personal communication; 206), which map proximal to the rDNA cluster. In addition, *ilv5* (148) maps distal to the rDNA genes and shows meiotic linkage to this cluster of genes. This linkage analysis was accomplished by integrating the *LEU2* gene into the rDNA sequences and then using this marker to score these repeated genes. The meiotic distance from *rDNA* to *ilv5* is over 100 cM. Distal, but linked, to *ilv5* is a group of genes whose order on the chromosome is still uncertain. The genes *nam2* (46), *SUP86* (68), *cup3* (Welch and Fogel, personal communication), and *mar2* (A. Klar, personal communication) have been added to the three genes already in this group. The mutations *mar2*, *ste8*, and *sir3* have been shown to be allelic (Klar, personal communication; R. Chan, personal communication). All three affect expression of the silent copies of the mating type locus. Finally, *sst1* is 7 cM distal to *mar2* (24; Chan, personal communication).

Chromosome XIII

Several changes have been made to the map of chromosome XIII since our last major review (132). The genes *eth2* and *met6*, which had tentatively been placed distal to *lys7* (117), have been found to be located on chromosome V near *trp2* (Schild and Mortimer, in press). The "*met5*" marker that was mapped in this location was, in fact, *met6*; *met5* has now been shown to map on chromosome X (Schild and

TABLE 15. New tetrad analysis data for chromosome XV[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
SUF1-arg8			113	1	90	23.6	2.3	56
SUF1-arg1			43	19	150	75.7	13.0	56
arg8-arg1			125	59	438	79.3	8.4	55, 56
adh1-arg8						45		M. Ciriacy, personal communication
adh1-arg1						27		M. Ciriacy, personal communication
glc4-arg1						15		J. Pringle, personal communication
SUF17-arg8			86	34	285	71.9	8.6	55
SUF17-arg1			375	0	23	2.9	0.6	55
pep12-tup4			69	0	17	9.9	2.2	G. Fabian and E. Jones, personal communication
pep12-cen15	71	15				9.2	2.2	G. Fabian and E. Jones, personal communication
pep12-mak1			61	0	25	14.9	2.7	G. Fabian and E. Jones, personal communication
tup4-mak1			46	0	40	23.6	2.9	G. Fabian and E. Jones, personal communication
tup4-cen15	56	30				19.6	3.3	G. Fabian and E. Jones, personal communication
mak1-cen15	76	10				6.0	1.8	G. Fabian and E. Jones, personal communication
spoT11-pet17			17	0	17	25.1	4.4	M. Tsuboi, personal communication
spoT11-arg1			9	1	23	45.1	11.0	M. Tsuboi, personal communication
spoT11-cen15	80	7				4.1	1.5	M. Tsuboi, personal communication
tup7-cen15	80	1				0.6	0.6	9
tup7-pho80			84	0	0	0		9
tup7-mak1			35	0	2	2.8	2.0	9
tup7-tup4			58	0	16	11.2	2.7	9
tup7-tmp1			13	0	18	29.9	5.3	9
top1-cen15	69	1				0.7	0.6	186
top1-pet17			7	0	7	25.2	7.0	186
suf11-cen15	150	192				35.5	2.5	56
suf11-pet17			278	0	66	9.7	1.1	56
suf11-cdc21			342	0	2	0.3	0.2	56
suf11-ade2			138	5	201	33.9	2.4	56
RAS^{sc}1-pet17			26	2	35	39.0	9.0	182
RAS^{sc}1-ade2			87	0	34	14.1	2.1	182
RAS^{sc}1-ade2			24	0	4	7.2	3.5	88
Total			111	0	38	12.8	1.8	
RAS^{cs}1-his3			8	3	15	105.4	111.4	88
spoT15-ade2			61	0	13	8.8	2.2	M. Tsuboi, personal communication
spoT15-pet17			31	0	29	24.2	3.3	M. Tsuboi, personal communication
spoT15-his3			12	6	53	73.4	19.4	M. Tsuboi, personal communication
smr3-ade2			42	0	66	30.8	2.5	50
smr3-his3			67	2	39	24.5	5.4	50
ste4-his3			10	0	3	11.8	6.3	166
ste4-met7			18	0	10	18.0	4.6	166
ste13-his3			11	0	15	29.9	5.9	D. Barnes and J. Thorner, personal communication
ste13-met7			16	0	11	20.5	4.8	D. Barnes and J. Thorner, personal communication
ste13-cdc31			10	1	12	42.8	20.3	D. Barnes and J. Thorner, personal communication
cdc31-ade2			12	5	46	69.8	19.3	Schild and Mortimer, in press
cdc31-his3			18	0	24	28.6	3.9	Schild and Mortimer, in press
cdc31-his3			13	2	18	52.9	24.3	D. Barnes and J. Thorner, personal communication
Total			31	2	42	37.1	7.3	

Continued on following page

TABLE 15-*Continued*

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (cM)	SE	
cdc31-met7			44	0	8	7.7	2.6	Schild and Mortimer, in press
cdc31-met7			17	0	16	25.1	5.1	D. Barnes and J. Thorner, personal communication
Total			61	0	24	14.2	2.5	
suf13-his3			43	8	147	51.3	5.4	35
suf13-tra3			128	1	77	20.2	2.2	35
suf13-prt1			48	11	155	55.2	6.4	35
his3-gcd1			86	1	113	29.8	2.3	35
cdc64-his3			8	10	45	NL		Hanic-Joyce, in press
cdc64-met7			9	0	20	34.6	4.4	Hanic-Joyce, in press
cdc64-prt1			46	1	67	32.1	3.4	Hanic-Joyce, in press
cdc66-cdc64			42	0	12	11.2	2.9	P. Hanic-Joyce and D. R. Carruthers, personal communication
cdc66-prt1			11	0	30	36.6	3.5	P. Hanic-Joyce and D. R. Carruthers, personal communication
cdc63-prt1			372	0	0	0		Hanic-Joyce, in press
phr1-prt1			43	0	16	13.6	2.9	161
phr2-phr1			27	0	16	18.7	3.7	112

[a] See footnote *a*, Table 1.

Mortimer, in press). Fragment V, containing *arg81*, *SUP5*, and *GAL80*, has been located on the left arm of chromosome XIII, using the *rad52* chromosome loss mapping method (Schild and Mortimer, in press). Independently this group of genes had been placed on chromosome XIII by showing that both *GAL80* and *SUP5* hybridize to the OFAGE-separated band corresponding to this chromosome (Carle and Olson, in press). *SUP79* (68) and *SUF22* (55) also map in this region, distal to *rad52*. *spoT2* maps very close to the centromere (191), whereas *tsm0111*, *sec59*, and *tsm0800*, respectively, map 1.9, 3.8, and 11.5 cM from the centromere on the right arm (10; Boutelet and Hilger, personal communication; Fields and Schekman, personal communication). *mcm1* is only 2 cM from *lys7* but the order of these two genes relative to *arg80* is unknown (G. Maine and B. Tye, personal communication). *sup113* maps 20.9 cM distal to *lys7* (Ono, personal communication), whereas *ilv2* is 38.2 cM distal to this marker (148; Hawthorne, personal communication). *pet-ts2858* maps 23.2 cM distal to *ilv2*. This petite mutation also shows loose linkage to *rna1* which serves to join the *SUP8-rna1* group meiotically to the rest of the chromosome and to orient this group, with *rna1* most proximal (116).

TABLE 16. New tetrad analysis data for chromosome XVI[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (CM)	SE	
spoT16-gal4			100	0	5	2.4	1.1	M. Tsuboi, personal communication
pep4-gal4			50	3	118	40.1	3.6	F. Park and E. Jones, personal communication
cdc60-gal4			37	6	98	50.0	6.9	Hanic-Joyce, in press
cdc60-pep4			36	0	3	3.9	2.3	Hanic-Joyce, in press
tsm0115-rad1			83	0	27	12.5	2.2	199
tsm0115-cen16	91	81				28.1	2.9	199
tsm0115-mak6			10	0	13	28.4	5.3	199
tsm0115-aro7			27	8	66	67.5	17.0	199
nib1-rad1			37	0	0	0		74
nib1-cen16	12	5				16.1	6.8	74
SUF21-cen16	159	3				0.9	0.5	55
SUF21-aro7			46	1	96	35.7	2.8	55
gln1-cen16	45	59				36.0	4.5	A. Mitchell, personal communication
gln1-mak6			28	1	24	29.0	7.4	A. Mitchell, personal communication
gln1-mak3			85	0	36	15.1	2.2	A. Mitchell, personal communication
gln1-aro7			155	0	72	16.0	1.6	A. Mitchell, personal communication
tsm0120-cen16	27	28				31.0	5.4	10; F. Boutelet and F. Hilger, personal communication
tsm0120-mak3			47	0	8	7.3	2.4	10; F. Boutelet and F. Hilger, personal communication
tsm0120-aro7			45	0	10	9.1	2.7	10; F. Boutelet and F. Hilger, personal communication
spoT20-aro7			22	0	1	2.3	2.5	191
spoT20-cen16	61	109				43.5	4.4	191
Ty1-aro7			19	4	52	54.7	11.6	92

[a] See footnote *a*, Table 1.

TABLE 17. New tetrad analysis data for chromosome XVII[a]

Interval	Segregation (no.)		Ascus type (no.)			Map distance		Reference
	FD	SD	PD	NPD	T	x' (CM)	SE	
KRB1-cen17	268	13				2.3	0.6	202
KRB1-cen17	20	1				2.4	2.4	199
Total	288	14				2.3	0.6	

[a] See footnote *a*, Table 1.

SUP78 (68) and *spoT7* (191) map close to *rna1*. *ade4* (Schild and Mortimer, in press) and *prc1* (E. Jones, M. Aynardi, and M. Kolodny, personal communication) have been shown to map distal to *SUP8*, with *ade4* probably the most distal. *adh3* maps 16 cM from *lys7* (M. Ciriacy, personal communication) and *adh2* is 8 kb (ca. 3 cM) removed from *ade4* (27). *cdc61* has been mapped 31.8 cM from *ade4* (Hanic-Joyce, in press). Finally, Celenza and Carlson (personal communication) have placed *SUC4* on chromosome XIII but have not mapped it to a specific location on this chromosome.

Chromosome XIV

In our earlier review (132), chromosome XIV was identified by the centromere-linked marker *pet8*, and *rna2* and *lys9* were located distal to *pet8* on the right arm. Also, near the centromere were *SUF10* and *spo1*. Another group of linked genes that included *mak26*, *ski4*, *hex2*, *petx*, and *ski3* had been located on this chromosome only by trisomic analysis. The markers *met4* and *met2* had been eliminated from all identified chromosomes, including XIV, by aneuploid analyses and hence assigned to chromosome XVII (130). Several genes were subsequently shown to be linked to markers on both of these "chromosomes." It has since been found that the original aneuploid analysis that established the independence of these chromosomes was faulty (90); the strain that was disomic for *met4* in fact contained two copies of the left arm of chromosome XIV and one copy of the right arm. This partial disome was crossed to *lys9*, a right arm marker, and 2:2 segregation for Lys^+:Lys^- was obtained, whereas disomic ratios for *met4* were observed. This indicated incorrectly that *met4* was not on the same chromosome as *lys9*. The *spo11* mapping method was subsequently used to show that all of these markers were on the same chromosome (90). This is another example of the pitfalls of aneuploid analysis as a mapping method. It is our view that assignment of a gene to a chromosome by this method must be considered provisional until confirmed by tetrad analysis or by mitotic crossing-over procedures.

To the combined chromosome XIV have been added *SUF6* distal to *met2* (56), *sec2* distal to *pet2* (Fields and Schekman, personal communication), and *fol1* and *rad50* proximal to *pet2* (93; Game, personal communication). In addition, *suf14* is 42 cM proximal to *pet2* (35). The genes *pms1* (M. S. Williamson, J. C. Game, and S. Fogel, Genetics, in press), $RAS^{sc}2$ (88), *top2* (K. Voelkel, S. DiNardo, and R. Sternglanz, manuscript in preparation), and *leu4* (L. L. Chang, P. R. Gatzek, and G. B. Kohlhaw, Gene, in press) all map near *met4*. These genes are of great interest: *pms1* leads to a considerable increase in the frequency of postmeiotic segregation, $RAS^{sc}2$ is a close analog of a human oncogene, and *top2* codes for or controls the synthesis of topoisomerase 2. *leu4* is one of two genes coding for α-isopropyl malate synthase (Chang et al., in press). Two Ty1

TABLE 18. Glossary of gene symbols

Symbol	Definition
act	Actin
ade	Adenine requiring
adh	Defective in alcohol utilization
adr	Alcohol nonutilizer
alg	Asparagine-linked glycosylation deficient
AMY	Antimycin resistance
anp	Sensitive to ANP and osmotic sensitive
ant	Antibiotic resistance
ard	Defective in cell cycle arrest at start
arg	Arginine requiring
aro	Aromatic amino acid requiring
asp	Aspartic acid requiring
ate	Arginyl-tRNA-protein transferase deficient
AXE	Axenomycin resistance
bar	a cells lack barrier effect on α factor
BOR	Borrelidin resistance
can	Canavanine resistance
car	Arginine catabolism defective
cdc	Cell division cycle blocked at 36°C
cen	Centromere
chl	Chromosome loss
cho	Choline requiring
cly	Cell lysis at 36°C
cpa	Arginine requiring in presence of excess uracil
cry	Cryptopleurine resistance
CUP/cup	Copper resistance
cyc	Cytochrome *c* deficiency
cyh	Cycloheximide resistance
cyr	Adenylate cyclase deficient
cys	Cysteine requiring
dal	Allantoin degradation deficient
dbl	Alcian blue dye binding deficient
dsm	Premeiotic DNA synthesis deficient
dur	Urea degradation deficient
eam	Phenotypic revertants of *cho1* mutants
erg	Defective in ergosterol biosynthesis; many also nystatin resistant
eth	Ethionine resistance
fas	Fatty acid synthetase deficient
fdp	Unable to grow on glucose, fructose, sucrose, or mannose
flk	Resistance to catabolite repression
FLO	Flocculation
fol	Folinic acid requiring
fro	Frothing
gal	Galactose nonutilizer
gcd	Depressed for general control of amino acid synthesis
gcn	Non-derepressible general control of amino acid synthesis
glc	Glycogen storage
glk	Glucokinase deficient (unable to use glucose)
gln	Unable to derepress glutamine synthetase
hem	Heme synthesis deficient
hip	Histidine-specific permease
his	Histidine requiring
HML	Mating type cassette
HMR	Mating type cassette
HO	Homothallic switching
hol	Histidinol uptake proficient
hom	Homoserine requiring
hxk	Hexokinase deficient
ils	Isoleucyl-transfer RNA synthetase deficient; no growth at 36°C
ilv	Isoleucine-plus-valine requiring
ino	Inositol deficient
kar	Nuclear fusion defective
kex	Unable to express killer phenotype

Continued on following page

TABLE 18—*Continued*

Symbol	Definition
KRB	Suppression of some *mak* mutations
lap	Leucine aminopeptidase deficient
let	Lethal
leu	Leucine requiring
lts	Low-temperature sensitive
lys	Lysine requiring
mak	Maintenance of killer deficient
MAL	Maltose fermentation positive
mar	Partial expression of mating type cassettes
MAT	Mating type locus
mcm	Minichromosome maintenance deficient
mes	Methionyl-transfer RNA synthetase defective; no growth at 36°C
met	Methionine requiring
mfα	α-mating factor
MGL	α-Methylglucoside fermenter
min	Inhibited by methionine
mnn	Mannan synthesis defective
mut	Elevated spontaneous mutation rate
nam	Nuclear suppressor of mitochondrial mutations
NHS	Hydrogen sulfide production inhibitor
nib	Nibbled colony phenotype due to 2μm DNA
nul	Nonmater
ole	Oleic acid requiring
oli	Oligomycin resistance
osm	Sensitive to low osmotic pressure
pdx	Pyridoxine requiring
pep	Proteinase deficient
pet	Petite; unable to grow on nonfermentable carbon sources
pgi	Phosphoglucose isomerase deficient
pgk	3-Phosphoglycerate kinase deficient
pha	Phenylalanine requiring
pho	Phosphatase deficient
phr	Photoreactivation repair deficient
PHS	Hydrogen sulfide production deficient
pms	Increased postmeiotic segregation
ppr	Defective in pyrimidine biosynthetic pathway regulation
prb	Proteinase B deficient
prc	Proteinase C deficient
prt	Protein synthesis defective at 36°C
pur	Purine excretion
put	Proline nonutilizer
pyk	Pyruvate kinase deficient
rad	Radiation (ultraviolet or ionizing) sensitive
RAS^{sc}	Homologous to *RAS* proto-oncogene
RDN	Ribosomal RNA structural genes
rev	Nonrevertible
rme	Meiosis independent of mating type heterozygosity
rna	Unable to grow at 36°C; block in RNA synthesis
ROC	Roccal resistance
sam	*S*-Adenosylmethionine deficient
sec	Secretion deficient
ser	Serine requiring
sir	Defective in regulation of silent mating type information
ski	Superkiller
SMR/smr	Sulfometuron methyl resistance
snf	Deficient in derepression of many glucose-repressible genes
sot	Suppression of deoxythymidine monophosphate uptake
spd	Sporulation not repressed on rich media
spe	Spermidine resistance
spo	Sporulation deficient
spt	Suppressor of *Ty*-mediated expression of *his4*
ssn	Suppressor of *snf1*
sst	Supersensitive to α factor
ste	Sterile
SUC	Sucrose fermenter
SUF/suf	Suppression of frameshift mutation
suh	Suppression of *his2-1*
SUP/sup	Suppression of nonsense mutation
SUS	Suppression of *ser1*
swi	Homothallic switching deficient
tcm	Trichodermin resistance
TEF	Translational elongation factor
thi	Thiamine requiring
thr	Threonine requiring
til	Thiaisoleucine resistance
tmp	Thymidine monophosphate requiring
top	Topoisomerase deficient
tra	Triazylalanine resistant
trn	Proline transfer RNA gene
trp	Tryptophan requiring
tsm	Lethal, temperature sensitive
tub	Tubulin; MBC resistance
tup	Deoxythymidine monophosphate uptake positive
tyr	Tyrosine requiring
umr	Non-ultraviolet revertible
ura	Uracil requiring

Continued

TABLE 18—*Continued*

sequences map between *met4* and the centromere (92). The gene *spo1* has been moved from the right to the left arm but is still very close to the centromere (di Domenico and Esposito, personal communication). Three genes have been mapped near *lys9*. These are *SUP28* (Ono, personal communication), *pet494* (138), and *hol1* (P. Farabaugh, personal communication). The order of these three genes relative to each other, *lys9*, or proximal markers is unknown.

Chromosome XV

Chromosome XV is one of the larger chromosomes of yeasts, with a physical size comparable to that of chromosome VII and with only chromosomes IV and XII larger (Carle and Olson, in press). Its meiotic length is about 375 cM and 39 genes have been mapped along it. Since our last review, the frameshift suppressors *SUF1* and *SUF17* have been added to the left arm (55, 56). In addition, *adh1* (Ciriacy, personal communication) and *glc4* (J. Pringle, personal communication) have been assigned to the *arg8-arg1* interval on this chromosome arm. *spoT11* is near the centromere on the left arm (191). The gene *mak1*, which had been mapped on the right arm near the centromere, has been shown to be an allele of *top1* (186), the gene that controls the synthesis of topoisomerase 1 of yeasts. Interestingly, either topoisomerase 1 or topoisomerase 2 is sufficient for most of the functions of the yeast cell cycle; topoisomerase 2 alone is necessary for separation of replicated chromosomes in mitosis (41). *mak8* has been shown to be allelic to *tcm1* (204), which had previously been mapped proximal to *pet17* (62). Very near to *tsm8740*, a cell cycle mutant, is $RAS^{sc}1$ a human oncogene analog (82, 182). It appears, however, that these genes are not alleles. A few map units distal to *tsm8740* is *spoT15* (191). Distal to *his3* are *ste4* (166) and *ste13* (D. Barnes and J. Thorner, personal communication), and *cdc31* maps further out on the chromosome distal to *met7* (Schild and Mortimer, in press). The recessive frameshift suppressor *suf13* is near *cpa1* (35) and distal to these genes is *cdc64* (Hanic-Joyce, in press). Both *suf13* and *cdc64* show linkage to *prt1*. This latter gene had earlier been located on chromo-

TABLE 19. List of mapped genes

Gene	Map position	Reference(s)
aas1	4R	See *gcn2*
aas2	11R	See *gcn3*
aas3	5R	See *gcn4*
act1	6L	49
ade1	1R	129, 158
ade2	15R	129
ade3	7R	82, 129, 185
ade4	13R	Schild and Mortimer, in press
ade5,7	7L	129, 140, 201
ade6	7R	69, 165; D. J. Plotkin, Ph.D. thesis, University of Chicago, Chicago, Ill., 1978
ade8	4R	2, 130; G. E. Jones, Ph.D. thesis, University of California, Berkeley, 1970
ade9	15R	37, 129
ADE15	7R	82
adh1	15L	M. Ciriacy, personal communication
adh2	13R	27; M. Ciriacy, personal communication
adh3	13R	M. Ciriacy, personal communication
adr1	4R	J. Wood and C. L. Denis, personal communication
alg1	2R	33
alg7	7R	6
AMY1	7L	110
AMY2	2L	110, 199
anp1	5L	123
ant1	7L	29
ard1	8R	M. Whiteway and J. Szostak, personal communication
arg1	15L	30, 71
arg3	10L	72
arg4	8R	69, 129, 198, 200
arg5,6	5R	53, 107, 129, 141; D. P. Morrison, Ph.D. thesis, University of Alberta, Edmonton, 1978
arg8	15L	71
arg9	5R	129
arg80	13R	72
arg81	13L	72; Schild and Mortimer, in press
arg82	4R	72
arg84	5R	79
aro1	4R	129, 130, 203
aro2	7L	129, 140, 165, 201
aro7	16R	70, 103, 145, 200
asp1	4R	83; Jones, Ph.D. thesis
asp5	12R	43, 78, 129, 150
ate1	7L	160
AXE1	7L	S. Sora, personal communication
bar1	9L	G. Sprague and I. Herskowitz, personal communication
BOR1	5R	141
BOR2	7L	141
can1	5L	130, 164, 200
car2	12R	72
cdc2	4L	66, 91, 130, 203
cdc4	6L	38, 130
cdc5	13L	38, 130
cdc6	10L	F. Hilger, personal communication; Kawasaki, Ph.D. thesis
cdc7	4L	130, 145
cdc8	10R	97, 130
cdc9	4L	66, 130
cdc10	3R	34, 130
cdc11	10R	97, 130
cdc12	8R	38, 200
cdc14	6R	38, 130
cdc15	1R	130
cdc16	11L	66, 203
cdc19	1L	Kawasaki, Ph.D. thesis

Continued

TABLE 19—*Continued*

Gene	Map position	Reference(s)
cdc21	15R	58, 200
cdc24	1L	85
cdc26	6R	Kawasaki, Ph.D. thesis
cdc28	2R	32, 66, 200
cdc29	9L	66
cdc31	15R	Schild and Mortimer, in press
cdc35	10R	See *tsm0185*
cdc36	4L	166
cdc37	4R	166
cdc39	3R	166
cdc40	4R	Y. Kassir, M. Kupiec, A. Shalom, and G. Simchen, personal communication
cdc43	7L	A. Adams and J. Pringle, personal communication
cdc60	16L	Hanic-Joyce, in press
cdc61	13R	Hanic-Joyce, in press
cdc62	7R	Hanic-Joyce, in press
cdc63	15R	Hanic-Joyce, in press
cdc64	15R	Hanic-Joyce, in press
cdc66	15R	P. Hanic-Joyce and D. R. Carruthers, personal communication
chl1	16L	108
cho1	5R	4, 107
cly2	2L	130, 199
cly3	6R	130
cly7	11L	130
cly8	7R	130; Plotkin, Ph.D. thesis
cpa1	15R	72
cry1	3R	61, 125, 170
CUP1	8R	69, 129
cup2	7L	J. W. Welch and S. Fogel, personal communication
cup3	12R	J. W. Welch and S. Fogel, personal communication
cup5	5L	J. W. Welch and S. Fogel, personal communication
cup14	4R	J. W. Welch and S. Fogel, personal communication
cyc1	10R	97, 130
cyc2	15R	158
cyc3	1L	158
cyc7	5L	164
cyc8	2R	158
cyc9	3R	158
cyh1	2L	129
cyh2	7L	129, 140, 165; Plotkin, Ph.D. thesis
cyh3	7L	129
cyh4	15R	129
cyh10	2R	167
cyr1	10R	121
cys1	1L	158, 203; S. Halos, Ph.D. thesis, University of California, Berkeley, 1976
cys3	1L	147
dal1	9R	31, 98
dal2	9R	31, 98
dal3	9R	T. G. Cooper and H. S. Yoo, personal communication
dal4	9R	31, 98
dal80	11R	192
dal81	9R	192
dbl1	11L	5, 54
dsm1	7R	D. Fast, Ph.D. thesis, University of Chicago, Chicago, Ill., 1978
dur1	2R	32
dur2	2R	32
dur3	8L	T. G. Cooper and M. Mojumdar, personal communication
dur4	8L	T. G. Cooper and M. Mojumdar, personal communication

Continued on following page

TABLE 19—*Continued*

Gene	Map position	Reference(s)
DUR80	2R	25
eam1	10L	3
erg6	4R	122
eth2(sam2)	5R	117, 118; Schild and Mortimer, in press
fas1	11L	16, 36
fdp1	2R	194
flk1	3R	175
FLO1	1R	75, 158, 177
FLO4	1R	See *FLO1*
fol1	14L	J. Game and J. Little, personal communication
fol2	7R	J. Game and J. Little, and B. Rockmill, personal communication
fro1	7R	184, 185
fro2	7R	184, 185
gal1	2R	8, 43, 107, 129
gal2	12R	43, 129, 150
gal3	4R	43, 80
gal4	16L	J. Haber, personal communication
gal5	F6	44
gal7	2R	8, 43, 107, 129
gal10	2R	8, 43, 107, 129
gal80	13L	Schild and Mortimer, in press; Carle and Olson, in press
GAL83	5R	120
gcd1(tra3)[a]	15R	73; D. Yep, Ph.D. thesis, Cornell University, Ithaca, N.Y., 1973
gcn2(aas1)	4R	73
gcn3(aas2)	11R	73
gcn4(aas3)	5R	73
glc1	2R	J. Pringle, personal communication
glc3	5L	J. Pringle, personal communication
glc4	15L	P. Oeller and J. Pringle, personal communication
glc6	2R	J. Pringle, personal communication
glk1	3L	115
gln1	16R	A. P. Mitchell, personal communication
gln3	5R	127
hem10	7L	193
hip1	7R	Tanaka and Fink, Abstr. Mol. Biol. Yeast Meet., 1983
his1	5R	53, 107, 129, 141; E. Savage, Ph.D. thesis, University of Alberta, Edmonton, 1979
his2	6R	40, 70, 129, 130
his3	15R	37, 129
his4A,B,C	3L	34, 69, 185, 196
his5	9L	107, 129, 144
his6	9L	69, 130, 144
his7	2R	129; Plotkin, Ph.D. thesis
his8	15R	See *his3*
HML	3L	65
HMR	3R	65
HO	4L	Kawasaki, Ph.D. thesis
hol1	14R	P. Farabaugh, personal communication
hom2	4R	129, 130
hom3	5R	52, 129, 141
hom6	10R	Schild and Mortimer, in press
hxk1	6R	109; Lobo, Ph.D. thesis
hxk2	7L	115
ils1	2L	124
ilv1	5R	76, 107, 129
ilv2	13R	148
ilv3	10R	70, 97, 129, 130
ilv5	12R	148
ino1	10L	42
kar1	14L	47, 90
kex1	7L	201
kex2	14L	188, 201

Continued

TABLE 19—*Continued*

Gene	Map position	Reference(s)
KRB1	17R	199
lap1	11L	190
lap3	14L	90, 190
lap4	11L	190
let1	1R	130
let1M	13R	139
let3	10L	139
let5	10L	139
let6	6L	139
leu1	7L	69, 109, 129, 165
leu2	3L	34, 69, 107, 129
leu4	14L	Chang et al., in press
lts1	7L	167
lts3	7L	167
lts4	4R	167
lts10	4R	167
lys1	9R	31, 69, 98, 107, 144
lys2	2R	32, 69, 129, 200; Plotkin, Ph.D. thesis
lys4	4R	R. Contopoulou, personal communication
lys5	7L	129, 140, 165, 201
lys7	13R	36, 66, 129, 130
lys9	14R	129, 130, 201
lys11	9L	107, 129, 144
mak1	15R	200
mak3	16R	145, 200
mak4	2R	200
mak5	2R	200
mak6	16R	145, 200
mak7	8L	197, 198, 200
mak8	15R	200
mak9	11L	203
mak10	5L	164, 200
mak11	11L	203
mak12	12L	203
mak13	9R	198
mak14	3R	203
mak15	11R	203
mak16	1L	203
mak17	10L	198
mak18	8R	198
mak19	8R	198
mak20	8L	198
mak21	4R	203
mak22	12L	198
mak24	7L	198
mak26	14L	198
mak27	13R	203
MAL1	7R	23, 82, 129, 185
MAL2	3R	12, 69, 109
MAL3	2R	114; Kawasaki, Ph.D. thesis
MAL4	11R	70, 129, 130, 203
mar1	4L	91
mar2(ste8)	12R	A. Klar, personal communication
MAT	3R	61, 69, 125, 129, 170
mcm1	13R	G. Maine and B. Tye, personal communication
mes1	7R	132
met1	11R	69, 129, 130
met2	14L	90, 130
met3	10R	97, 129, 145
met4	14L	90, 130
met5	10R	Schild and Mortimer, in press
met6	5R	117, 118; Schild and Mortimer, in press
met7	15R	Lowenstein, Ph.D. thesis
met8	2R	32, 70, 129
met10	6R	40, 107, 109, 129; Kawasaki, Ph.D. thesis
met13	7L	129, 140, 165, 168, 201

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TABLE 19—*Continued*

Gene	Map position	Reference(s)
met14	11R	66, 77, 129, 203
met20	11R	119
mfα2	7L	C. Shari and J. Kurjan, personal communication
MGL2	2R	114; Kawasaki, Ph.D. thesis
min1	5L	164
mnn1	5C	1
mnn2	2R	5
mnn4	11L	5
mut1	F11	60
mut2	F11	60
nam2	12R	46
NHS1	5R	180
nib1	16L	74
nul3	4R	130
ole1	7L	155, 165
oli1	7L	159
osm1	10R	168
osm2	16R	168
pdx2	F6	69
pep3	12R	206; E. Jones, personal communication
pep4	16L	F. Park and E. Jones, personal communication
pep7	4R	E. Jones and M. Kolodny, personal communication
pep12	15L	G. Fabian and E. Jones, personal communication
pep16	12R	E. Jones, personal communication
pet1	8R	69, 129
pet2	14L	90, 129, 130
pet3	8R	38, 130, 198, 200
pet8	14R	38, 129, 130, 201
pet9	2L	43, 129, 142
pet11	2R	32, 70, 129
pet14	4R	130, 203
pet17	15R	70, 130, 158, 200
pet18	3R	130, 200
pet494	14R	138
pet-ts1402	5R	116
pet-ts2858	13R	116
petx	14L	201
pgi1	2R	114
pgk1	3R	95
pha2	14L	90, 129, 130
pho2	4L	187
pho3,5	2R	64, 171, 183, 189
pho4	6R	187
pho8	4R	86
pho80	15R	9
PHO82	6R	187
pho85	16L	187
phr1	15R	161
phr2	15R	112
PHS1	4R	179
pms1	14L	Williamson et al., in press
ppr1	12R	104
prb1	5L	207
prc1	13R	E. Jones, M. Aynardi, and M. Kolodny, personal communication
prt1	15R	130
prt2	14L	90, 130
prt3	5L	130
pur5	4R	2
put2	8R	11
pyk1	1L	113, 158, 174
r_s^1	5R	See *rad24*
rad1	16L	108, 153, 154
rad2	7R	132
rad3	5R	172; Morrison, Ph.D. thesis

Continued

TABLE 19—*Continued*

Gene	Map position	Reference(s)
rad4	5R	172; Morrison, Ph.D. thesis
rad5	12R	99
rad6	7L	59
rad7	10R	97
rad9	4R	Dowling, Ph.D. thesis
rad18	3R	130, 158
rad23	5L	123
rad24	5R	F. Eckardt and J. Game, personal communication
rad50	14L	93; J. Game, personal communication
rad51	5R	Morrison, Ph.D. thesis
rad52[a]	13L	154
rad54	7L	J. Game, personal communication; Dowling, Ph.D. thesis
rad55	4R	130
rad56	16R	59
rad57	4R	59, 145
RAS^{sc}*1*	15R	88, 182
RAS^{sc}*2*	14L	88; L. Robinson and K. Tatchell, personal communication
RDN1	12R	150
rev2	12R	See *rad5*
rev5	10R	C. W. Lawrence, personal communication
rev7	9L	C. W. Lawrence, personal communication
rme1	7R	156
rna1	13R	130, 198, 203
rna2	14R	38, 130, 201
rna3	4R	130
rna5	2R	130; Kawasaki, Ph.D. thesis
rna6	2R	See *tsm7269*
rna11	4L	130, 187, 203
ROC1	12R	129
sam2 (*eth2*)	5R	117, 118; Schild and Mortimer, in press
sec1	4R	C. Fields and R. Schekman, personal communication
sec2	14L	C. Fields and R. Schekman, personal communication
sec3	5R	C. Fields and R. Schekman, personal communication
sec4	6L	C. Fields and R. Schekman, personal communication
sec5	4R	C. Fields and R. Schekman, personal communication
sec7	4R	C. Fields and R. Schekman, personal communication
sec18	2R	C. Fields and R. Schekman, personal communication
sec55	3R	C. Fields and R. Schekman, personal communication
sec59	13R	C. Fields and R. Schekman, personal communication
ser1	15R	129; J. R. Johnston, Ph.D. thesis, University of California, Berkeley, 1962; Lowenstein, Ph.D. thesis
ser2	7R	82
sir1	11R	J. M. Ivy, personal communication
sir2	4L	See *mar1*
sir3	12R	See *mar2* and *ste8*
sir4	4R	J. M. Ivy, personal communication
ski1	7L	188
ski3	14L	188
ski4	14L	188
SMR1	13R	50
smr2	7L	50
smr3	15R	50
snf1	4R	22
sot1	16L	153

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TABLE 19—*Continued*

Gene	Map position	Reference(s)
spd1	15L	I. Dawes, personal communication
spe2	15L	30, 71
spo1	14L	90; B. DiDomenico and R. E. Esposito, personal communication
spo7	1L	R. E. Esposito and C. Waddell, personal communication
spo11	8L	S. Klapholz and R. E. Esposito, personal communication
spo12	8R	89
spo13	8R	S. Klapholz and R. E. Esposito, personal communication
spo14	11R	M. Townsend, B. DiDomenico, S. Klapholz, and R. E. Esposito, personal communication
spoT1	13C	M. Tsuboi, personal communication
spoT2	7L	M. Tsuboi, personal communication
spoT4	4L	191
spoT7	13R	M. Tsuboi, personal communication
spoT8	2R	191
spoT11	15L	M. Tsuboi, personal communication
spoT15	15R	M. Tsuboi, personal communication
spoT16	16L	M. Tusboi, personal communication
spoT20	16R	191
spoT23	11R	191
spt2	5R	205
spt3	4R	205
ssn2	4R	21
ssn6(cyc8)	2R	21
sst1	9L	R. K. Chan, personal communication
sst2	12R	R. K. Chan, personal communication
ste4	15R	166
ste5	4R	166
ste7	4L	166
ste8(mar2)	12R	R. K. Chan, personal communication
ste9	4R	See *sir4*
ste13	15R	D. Barnes and J. Thorner, personal communication
SUC1	7R	23, 82, 129, 157, 185
SUC2	9L	107, 129, 144
SUC3	2R	114; Kawasaki, Ph.D. thesis
SUC5	4L	20; Kawasaki, Ph.D. thesis
SUF1	15L	56
SUF2	3R	34
SUF3	4R	56
SUF4	7R	23, 56
SUF5	15R	37
SUF6	14L	56
SUF7	13L	38
SUF8	*8R*	*38*
SUF9	6L	38
SUF10	14L	38
suf11	15R	56
suf12	4R	35
suf13	15R	35
suf14	14L	35
SUF15	7R	55
SUF16	3R	55
SUF17	15L	55
SUF18	6R	55
SUF19	5L	55
SUF20	6R	55
SUF21	16R	55
SUF22	13L	55
SUF23	10R	55
SUF24	4R	55
SUF25	4L	55, 56
suh2	12R	130
SUP-1A	11R	17

Continued

TABLE 19—*Continued*

Gene	Map position	Reference(s)
SUP2	4R	130
SUP3	15L	70, 71
SUP4	10R	97, 130; R. Gilmore, Ph.D. thesis, University of California, Berkeley, 1966
SUP5	13L	45; Schild and Mortimer, in press
SUP6	6R	40, 70, 130
SUP7	10L	70; Gilmore, Ph.D. thesis
SUP8	13R	130, 198
SUP11	6R	40, 70, 130
SUP15,16	16R	70, 103, 145
SUP17	9L	144
SUP19,20	5R	130, 145
SUP22	9L	144
SUP25	11R	70, 130
SUP26	12R	145
SUP27	4R	145
SUP28	14R	B. Ono, personal communication
SUP29	10C	145
SUP30	10C	130
SUP33	11L	B. Ono, personal communication
sup35	4R	129
sup36	4R	143
SUP37	12R	B. Ono, personal communication
SUP38	7L	B. Ono, personal communication
sup45	2R	70, 171
SUP46	2R	143, 146
sup47	2R	143
SUP50	F6	129, 130
SUP51	10C	130
SUP52	10C	102
SUP53	3L	152; C. Reed and S. Liebman, personal communication
SUP54	7L	101, 152; C. Reed and S. Liebman, personal communication
SUP56	1R	101
SUP57	6R	101
SUP58	11L	101
SUP61	3R	12, 130
SUP71	5R	130
SUP72	2R	68
SUP73	10L	68
SUP74	10L	68
SUP75	11L	D. Hawthorne, personal communication
SUP76	7R	68
SUP77	7R	68
SUP78	13R	68
SUP79	13L	68
SUP80	4R	68
SUP85	5R	68
SUP86	12R	68
SUP87	2R	68
SUP88	4R	68
sup111	8R	B. Ono, personal communication
sup112	7R	B. Ono, personal communication
sup113	13R	B. Ono, personal communication
SUS1	5L	129
swi1	16L	63; J. Haber and L. Rowe, personal communication
tcm1	15R	62, 204
TEF2	2R	162
thi1	F6	45, 129, 130
thr1	8R	69, 129
thr4	3R	95, 97, 100, 129, 181, 196
til1	7L	J. I, Stiles and F. Sherman, personal communication
tmp1	15R	13, 58, 200
top2	14L	K. Voelkel, S. DiNardo, and R. Sternglanz, personal communication

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TABLE 19—*Continued*

Gene	Map position	Reference(s)
tra3[a]	15R	73; D. Yep, Ph.D. thesis, Cornell University, Ithaca, N.Y., 1975 (see *gcd1*)
trn1	1R	C. Cummins and M. Culbertson, personal communication
trp1	4R	43, 59, 67, 129, 130, 145, 203
trp2	5R	53, 107, 129, 141
trp3	11L	5, 16, 36, 129, 203
trp4	4R	83, 130; Jones, Ph.D. thesis
trp5	7L	69, 129, 140, 141, 155, 165, 168; Plotkin, Ph.D. thesis
tsm1	3R	G. Sprague and J. Herskowitz, personal communication
tsm5	3R	G. Fink, personal communication; J. McCusker and J. Haber, personal communication
tsm0039	5R	10
tsm0070	6L	10
tsm0080	4R	10
tsm0111	13R	10
tsm0115	16L	200
tsm0119	7L	10
tsm0120	16R	10
tsm134	2R	64, 114, 130
tsm0139	9L	10
tsm0151	8R	10
tsm0185 (*cdc35*)	10R	10
tsm0186	8R	10
tsm0225	4L	F. Hilger, personal communication
tsm437	7L	130
tsm0800	13R	10
tsm4572	16R	72
tsm5162	4R	10
tsm7269 (*rna6*)	2R	72
tsm8740	15R	72
tub2	6L	J. Thomas, S. C. Falco, and D. Botstein, personal communication
tup1	3R	100, 196
tup4	15L	200
tup7	15R	9
tyr1	2R	32, 64, 129, 158; Plotkin, Ph.D. thesis
umr7	3R	100
ura1	11L	5, 16, 34, 129, 203
ura2	10L	130; Kawasaki, Ph.D. thesis
ura3	5L	1, 4, 129, 130, 164
ura4	12R	130, 150

[a] The reference to the mapping of *rad52* and *tra3* (*gcd1*) was incorrect in our previous review (132). *rad52* was mapped by M. Resnick (154) and *tra3* was mapped by D. Yep (Ph.D. thesis, 1975).

(130). The cell division cycle mutation *cdc63* has also been mapped in this region and has been shown to be allelic with *prt1* (Hanic-Joyce, in press). At 13.6 cM from *prt1* is *phr1* (161), although the order of these two genes on the chromosome is still unknown. It has also been reported that *phr2* is linked to *phr1* at a distance of 18 cM (112).

Chromosome XVI

gal4 is the most distal marker on the left arm of chromosome XVI; close to this gene is the sporulation-defective gene *spoT16* (191). About 40 cM proximal to *gal4* is *pep4* (E. Jones, personal communication) and 3.9 cM from *pep4* is the cell cycle mutant *cdc60* (Hanic-Joyce, in press). This group of genes had been located on the left arm of chromosome XVI because *gal4* shows mitotic linkage to *rad1* (J. McCusker and J. Haber, personal communication); however, no meiotic linkage exists between *gal4* and *rad1*. Neither *pep4* nor *cdc60*, the two most proximal genes of this group, has been tested for linkage against other more proximal left arm markers. To this proximal group of genes have been added *tsm0115* (199) and *nib1* (74). The frameshift suppressor *SUF21* is approximately 1 cM from the centromere on the right arm (55). Distal to *mak6* are *gln1* (A. Mitchell, personal communication) and *tsm0120* (Boutelet and Hilger, personal communication). Finally, a Ty1 sequence maps approximately 55 cM distal to *aro7* (92), which places it near *rad56*.

TABLE 20. Genetic and physical sizes of yeast chromosomes

Band	Chromosome	Recombinant length (cM)	DNA $\times 10^{-16}$ g[a]	DNA (kb)[b]	DNA (kb)[c]
1	I	98	14	198	260
2	VI	137	16	225	290
3	III	137	22	311	370
4	IX	198	35	495	460
5a	VIII	183	45	635	580
5b	V	233	50	709	580
6	XI	242	54	763	700
7	X	200	59	835	
8	XIV	283	61	864	
9	II	244	67	948	
10	XIII	229	70	991	
10b	XVI	176	74	1,047	
11a	XV	361	81	1,146	
11b	VII	391	91	1,285	
12	IV	485	111	1,571	
(13)	XII[d]	294	155	2,194	

[a] DNA content/meiotic bivalent (4c), assuming 250 $\times 10^{-16}$ g per haploid genome (94).
[b] DNA content/chromosome, assuming 14,000 kb per haploid genome (96).
[c] As determined from size standards, using OFAGE (Carle and Olson, in press).
[d] See discussion of chromosome XII.

Chromosome XVII

Chromosome XVII is identified only by the centromere-linked marker *KRB1* (killer replication bypass) (199, 202). As shown in these studies, this marker arises spontaneously in *mak7* segregants from crosses that carry the killer plasmid. Such segregants normally are killer minus (K^-) because *mak7* strains cannot maintain the killer plasmid. *KRB1* is a chromosomal mutation that in effect suppresses the *mak7* mutation. It is tightly centromere linked (<2 cM) and is not linked to markers near the centromeres of chromosomes I to XVI. *KRB1* strains have normal killer plasmids and normal killer double-stranded RNA. Also, *KRB1* does not appear to be a translational-type suppressor. However, the behavior of *KRB1* is not typical of mutations in nuclear genes. It arises at a high frequency in cells or segregants of cells that carry the killer plasmid. Also, it disappears when *mak7 KRB1* cells are grown at 37°C or are exposed to cycloheximide, treatments known to cure cells of the killer plasmid. Finally, a cross between two *mak7 KRB1* strains, which should yield 4:0 segregations for killer-nonkiller, more frequently yields 2:2 segregations, and experiments indicate that one of the two *KRB1* mutations has been lost.

If chromosome XVII, as defined by *KRB1* were "normal," i.e., typical of chromosomes I to XVI, one would expect to find centromere-linked genes on this chromosome at a frequency similar to that seen for the other chromosomes. For chromosomes I and XVI there are 144 markers within 25 cM of the centromere (centromere linked) for an average of 9 centromere-linked markers per centromere (range, 4 to 17). Assuming random association of markers

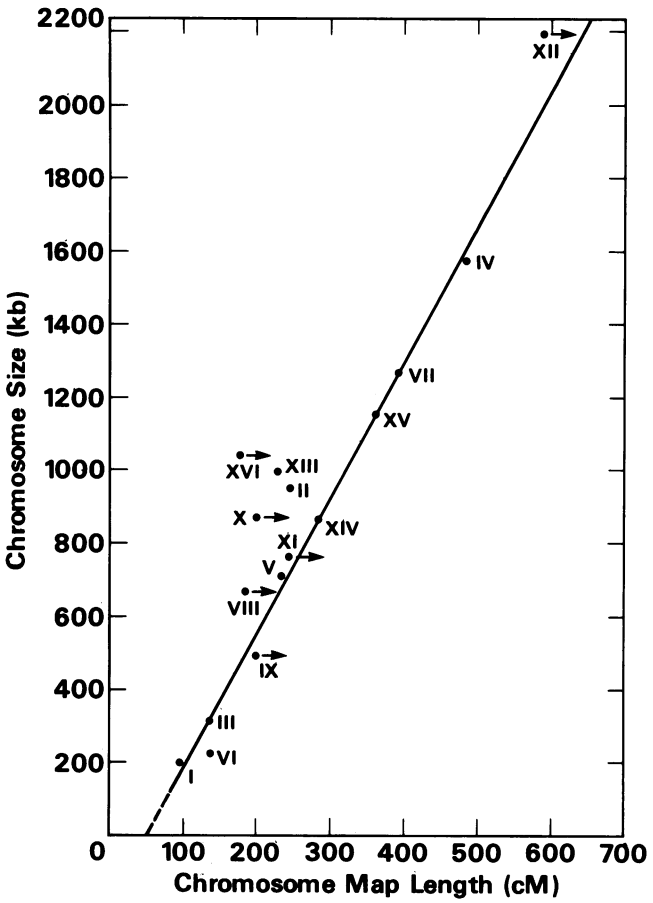

FIG. 2. Plot of chromosome sizes versus genetic map lengths. The points with arrows to the right represent minimum map lengths; these six chromosomes have regions whose lengths have not been determined by tetrad analysis.

with centromeres and equal probabilities of association/centromere, the probability of finding a centromere with only one centromere marker is very small ($<10^{-3}$).

Two recent studies which permit identification of individual chromosomes have found evidence for only 16 chromosomes. OFAGE reveals only 16 chromosomal bands (Carle and Olson, in press) and DAPI (4',6-diamidino-2-phenylindole) staining of meiotic bivalents also reveals only 16 such structures (94). One must conclude that the chromosome identified by *KRB1* is anomolous. Although it segregates at the first meiotic division, it fails to do so regularly. It appears and disappears in a manner completely atypical of nuclear genes. Also, were chromosome XVII typical of the other chromosomes, several other genes by now would have been found to be linked to *KRB1*. This presents a dilemma.

A possible explanation, which has features similar to one proposed by Wickner and Leibowitz (202), is that *KRB1* is located on a small linear or circular piece of DNA that also contains sequences that behave as a centromere. This piece of DNA could be a reverse transcript of all or a portion of the killer double-stranded RNA. This could account for the high frequency of appearance of *KRB1* in cells containing such RNA. Its small size would account for its instability in certain circumstances just as *cen* plasmids are somewhat unstable (28). The OFAGE and DAPI staining experiments, discussed above, may have been carried out on killer-minus strains which lack this small chromosome.

DISCUSSION

The genetic map of *S. cerevisiae* presented in this article describes the location of 568 genes distributed over 16 metacentric chromosomes plus a single gene, *KRB1*, located on a 17th chromosome. Since our last major review (132), 251 genes have been added to the genetic map. In addition, several linkages which had been established only by mitotic or aneuploid analyses have been confirmed by tetrad analysis. Only chromosomes VIII, IX, X, XI, XII, and XVI remain with regions not confirmed by tetrad analysis. Assuming a minimum of 100 cM for these regions, the total minimum length of the yeast map is now 4,500 cM, which is 100 cM less than our estimate made 5 years ago. This and the fact that the total number of mapped genes has increased by 79% argue that the current lengths of the yeast chromosomes are close to their actual lengths.

As discussed in detail above, three chromosomes have undergone major revisions since our last review. These are chromosomes VII, XIII, and XIV. On the right arm of chromosome VII, a large group of genes has been reversed in order relative to the centromere on the basis of meiotic linkage between *SUF4* and *cly8*. This places *SUC1/MAL1* as the most distal markers on this chromosome, where before this pair had been assigned as the proximal-most genes located distal to *cly8*. Chromosome XIII has had several major changes. The genes *eth2* and *met6* have been moved to chromosome V and the group of genes on the right arm, which had been located on this chromosome by mitotic analyses, has been shown to be meiotically linked to genes nearer the centromere. A group of genes previously identified as fragment V has been shown to be located on the left arm of this chromosome, and several other genes identified with this chromosome or fragment have been assigned to specific sites. Altogether, 17 genes have been added to this chromosome and its length has been extended to 229 cM. The most significant change on the genetic map since our last review is the joining of chromosomes XIV and XVII. These were incorrectly identified as separate chromosomes on the basis of aneuploid analyses, but subsequent studies showed that they were in fact parts of a single chromosome. This combined chromosome is metacentric and is one of the medium-sized chromosomes of yeasts. Another significant change is the substitution of *KRB1* as the centromere marker to define chromosome XVII. This is still problematical because of the anomalous genetic behaviour of this gene (see comments on chromosome XVII).

By and large, functionally related genes in yeasts are distributed somewhat randomly over the yeast genome. For example, the five genes involved in tryptophan biosynthesis are located on five different chromosomes. Nevertheless, there are some notable exceptions. On chromosome III, three enzymatic activities in histidine biosynthesis are clustered at the *his4* locus. In fact, this gene codes for a single polypeptide that has all three activities. The three genes *gal7*, *gal10*, and *gal1* are tightly linked on chromosome II, yet they do not represent an operon in the bacterial sense. All three genes are independently under the control of a fourth gene, *gal4*, located on chromosome XVI. This gene, in turn, is regulated by *GAL80*, located on chromosome XII. On chromosome V is located the *arg5-arg6* cluster. These genes appear to be under the control of the tightly linked gene *arg80* in an operon-like assembly, although it has been argued that this group also is not like a bacterial operon. A complete review of genetic regulation in yeasts with appropriate references has been presented by Jones and Fink (81).

Two remarkable developments have added new dimensions to our throughts about the yeast genome; both of these have appeared within the last year or two. A new procedure for gel electrophoresis allows separation of individual chromosomes (163; Carle and Olson, in press). In addition, a procedure involving DAPI staining has permitted identification of individual meiotic bivalents (94). By use of the novel gel electrophoresis procedure, Carle and Olson (in press) have electrophoretically resolved 16 chromosomal bands (albeit by using four strains) and have identified each of these with particular chromosomes by probing Southern blots with clones of genes known to be located on particular chromosomes. No evidence for a 17th chromosome could be found. The DAPI staining procedure clearly resolved 16 meiotic bivalents and photographs of these were scanned to determine their relative sizes. These sizes were calibrated by assuming the DNA content of a haploid as 250×10^{-16} g (1.56×10^{10} daltons). With this value, sizes ranged from 14×10^{-6} to 155×10^{-16} g per bivalent. A more accurate value for the DNA content of a haploid genome is 0.9×10^{10} daltons (96), which leads to a chromosomal size range of 198 to 2,194 kb. By assuming the same order, small to large, as determined by the electrophoretic and DAPI staining methods, it was possible to assign a physical size to each of the chromosomes (Table 20). This chromosomal size (converted to kilobases) is plotted against genetic map length in centimorgans (Fig. 2). A remarkable linear relation between physical size and recombination length is observed, and the slope of this line is 3.6 kb/cM. Lauer et al. (96) estimated the size of the largest yeast chromosome to be 1.5×10^9 to 2.2×10^9 daltons (2,200 to 3,330 kb). These values are in reasonable agreement with the estimated size of chromosome XII (Table 20).

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ADDENDUM IN PROOF

The centromere-linked gene *rad57* has recently been shown to map on the left arm of chromosome IV proximal to *rna11* instead of on the right arm (R. Contopoulou and R. Mortimer, unpublished data) and *cdc29* has been mapped distal rather than proximal to *his6* on chromosome IX (G. Basile and R. K. Mortimer, unpublished data). The previous edition of the genetic map (136) mistakenly identified the *ssn6* marker on chromosome II as *ssn1*; *ssn1* has not been mapped yet (M. Carlson, personal communication).

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